

Microbial biogeography: is everything small everywhere?

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Abstract

The distribution of microscopic organisms (that is, those smaller than 2 mm) has been historically considered non relevant for biogeography, because of the idea that due to their small size, dispersal abilities, resting stages and quick reproductive rates, the presence of microscopic organisms in any place was not limited by geographical barriers and distances. Recent studies challenge this idea, and provide theoretical and empirical evidence in support of the existence of spatial patterns at different scales, and of biogeographical processes affecting many groups of microscopic organisms. Here we review the current state of the art for microbial biogeography, summarising sources of problems and misconceptions, but also their solutions advancing the general understanding of biogeography, and conclude suggesting new avenues for future research.

1. Introduction

Microbial biogeography, the study of the distribution of microscopic organisms (smaller than 2 mm), is a relatively young discipline. Although the first attempts to describe microbial distribution date from the first decades of the Twentieth Century, the topic has not received much attention until the 1990s. Only recently, microbial biogeography has gained renewed vigour because of the resurgence of the ‘Everything-is-Everywhere’ hypothesis (Finlay, 2002; Fenchel & Finlay 2003; Finlay & Esteban, 2007; see O’Malley, 2008 and Williams, 2011 for historical reviews of this idea). We will not deal with the discussion on whether it is a true hypothesis in strict terms, as “regardless of detail or explanation, the phrase ‘everything is everywhere’ is clearly false, and in any case, one would need to know in what sense the words ‘everything’ and ‘everywhere’ are intended. As soon as something is not found everywhere then everything (obviously) is not everywhere. This much could be easily agreed upon” (quotation from Williams, 2011). Notwithstanding ambiguities and semantic problems, this idea produced interesting theoretical and empirical studies, which we will summarize in the next sections, dealing with what we know about the effect of size, taxonomy and space in microbial biogeography; then, we describe the empirical evidence on different group of organisms and conclude with potential consequences and challenges. Knowing if and how microscopic organisms

attain global distributions is a far reaching topic, going further than biogeography itself. For example, is speciation happening also in the absence of geographical barriers that would isolate populations? Here we introduce and discuss this and other key topics of current research in microbial biogeography, summarising the recent review of Fontaneto (2011).

2. Size

Size is one of the major drivers of most biological properties. The size of a living organism largely determines its shape, how it interacts with the environment and most (if not all) biological functions or its life history (Calder, 1996; Bonner, 2006). Importantly, the differences in body size result in profound biological differences, because the relationship between the volume and surface of organisms is non linear. Small increments in body surface result in large increments in volume; as a consequence, larger organisms have to regulate their temperature, osmosis, physiology, metabolism in a radically different way than small ones (Schmidt-Nielsen, 1984; Peters, 1986). Body size also plays a major role in determining the ecology of each species or individual, from their behaviour to the communities they interact with or the ecosystems where they live in, and even their extinction risk (Colinvaux, 1978; Cardillo & Bromhan, 2001; Hildrew et al., 2007). As a consequence, current research in many areas attempts to develop empirical and/or theoretical models relating biological patterns and processes with body size. This has resulted in the development of a large body of theory on the relationship between size and metabolism, based on universal scaling laws (Brown & West, 2000; Brown et al., 2004). Although to date such theory has failed to describe natural patterns when put to the test (e.g., Muller-Landau et al., 2006; Hawkins et al., 2007; Martínez del Río, 2008), current knowledge on many of the biological constraints imposed by body size is fairly good.

A notable exception to this general trend is the biogeographical implication of body size. Geographical variations in the body size of large organisms are relatively well known. As early as the mid Nineteenth Century, Bergmann (1847) proposed that populations of endothermic animals located at different latitudes differ in their body mass, increasing with latitude and colder climate (the so-called Bergmann's rule, see Meiri & Dayan, 2003). This formulation has been extended to the species level, as well as to ectotherms (e.g., Olalla-Tárraga et al., 2006); in short, for many animal

groups within closely related species the larger in size will be found at higher latitudes. The exact mechanisms behind this common (but not universal) trend are still elusive, for the origin of such latitudinal gradient may be related to many factors and to past climate changes, rather than just to current climate (Diniz-Filho et al., 2009). This rule, and many of the biogeographical patterns already described for large organisms do not scale down to microscopic organisms. Rather than a gradient in the patterns of diversity from large (macrobes) to small organisms (microbes), the general idea is that there may be an abrupt distinction between their biogeographical patterns.

The differences in the biogeographical patterns shown by microbes and macrobes have led to the hypothesis of a strong distinction in patterns and processes between macroscopic organisms with biogeography and microscopic organisms without biogeography (Finlay, 2002; Fenchel & Finlay, 2004). The threshold distinguishing these two size groups has been empirically defined to fall somewhere between 1 and 10 mm, although there is a general agreement that 2 mm would be the most adequate value (Finlay, 2002; Fenchel & Finlay, 2004). The biological assumption underlying this abrupt threshold is that microscopic organisms (and also macroscopic organisms with microscopic propagules such as fungi or bryophytes) are really different from larger ones (Fontaneto, 2011): they are so small that they can be passively dispersed everywhere, produce resting stages that allow them to survive adverse conditions and persist in any habitat, and can use asexual or parthenogenetic reproduction to quickly increase in number. According to the so-called 'Everything-is-Everywhere' hypothesis (Beijerinck, 1913; Baas-Becking, 1934; Finlay, 2002; Fenchel & Finlay, 2003; de Wit & Bouvier, 2006), these peculiar features would allow many microscopic organisms to attain cosmopolitan distribution. Such cosmopolitanism is quite uncommon in large organisms, implying that the biogeographic principles derived from macrobes are not general, and therefore that new hypotheses and theory shall be developed for microbes (Jenkins et al., 2011). However, the hypothesis that for microscopic organisms everything is everywhere ('ubiquity hypothesis') is considered too simplistic in the current scientific discussion, in opposition to the 'moderate endemism model' proposed by Foissner (1999, 2006), which suggests that many microscopic organisms have indeed restricted distributions, mostly in connection to their ecological traits other than size (e.g. Faurby & Funch, 2010; Foissner, 2011).

3. Current challenges to microbial biogeography

The basic units for any biogeographical analysis are records of the presence of species (or any other biological entity) and species lists (see Hortal, 2008). This poses two fundamental challenges to the development of microbial biogeography. On one hand, identifying microbial 'species' and/or defining meaningful units of diversity. On the other, linking spatial patterns with processes based on recorded presences.

3.1. Taxonomy

Most studies supporting the ubiquity hypothesis use morphological characteristics to identify the taxonomic units under consideration (Fenchel & Finlay, 2006). However, finding reliable morphological taxonomic characters for most microscopic organisms is notoriously difficult, so the use of morphological features may result in lumping together biological entities with distinct ecological and biogeographical attributes. This constitutes a fundamental problem, as units of diversity need to be unambiguously defined to map their distribution (Bass & Boenigk, 2011; Lacap et al., 2011). Thus, many species considered cosmopolitan may in fact represent complexes of cryptic species with restricted distributions. There are ways to solve this problem, and new tools help providing reliable estimates of diversity. Molecular taxonomy helps morphological taxonomy to reveal the existence of species complexes, and can potentially identify the correct units of diversity (that is, distinct evolutionary entities) within them (Pons et al., 2006; Burns et al., 2008; Barraclough et al., 2009). Additionally, environmental sequencing (by either cloning PCR products or ultrasequencing) is providing distributional data of many taxa otherwise unrecorded or undistinguished (e.g. Robeson et al., 2009; Creer et al., 2010).

3.2. Spatial patterns

For microscopic organisms, it will be difficult to disentangle the contribution of historical vs. ecological biogeography (Bass & Boenigk, 2011). Both large and small organisms present small discrepancies between their potential and realised distributions (that is, all the places where they could live in opposition to all the places where they actually live). However, they do it in a radically different way. The realised distribution of macrobe species usually constitutes a subset of their potential distribution, because most of them do not occupy all the places suitable for them (i.e. their distributions are not in equilibrium with the environment; see Araújo & Pearson,

2005). Absence from suitable places could be caused by a number of factors, such as historical effects, limitations to dispersal, or the presence of competitors (see Soberón, 2007, 2010; Soberón & Nakamura, 2009; Lobo et al., 2010). In contrast, the realised distribution of microscopic species may be larger than its potential distribution, because they are often present in areas that are not ecologically optimal for them thanks to their dispersal abilities and their capacity to survive as resting stages (Ganter, 2011; Marchant et al., 2011). This rarely happens in macroscopic organisms, and when it does it happens in areas placed nearby suitable sites, as a result of metapopulational processes (see Soberón & Nakamura, 2009). It follows that disentangling the effects of historical and ecological processes on the geographic distributions of microbes may prove to be an extremely difficult task. Moreover, it highlights the role of the mode of dispersal in creating fundamental differences between the biogeographies of small and large organisms, being also one of the main difficulties in supporting or falsifying the ubiquity hypothesis.

To further complicate the scenario, almost all studies and reviews on the biogeography of microscopic organisms report both evidence of large distributions and of endemic, restricted distributions. The same is true for phylogeographic analyses using DNA sequences to investigate the spatial patterns of distribution, which provide evidence of both long-distance gene flow and restricted gene flow (see reviews for different groups in Artois et al., 2011; Guil, 2011; Medina et al., 2011; Werth, 2011).

In addition to this, the little knowledge on the spatial patterns of variation in microbial communities is scattered among different types of analyses and measurements, such as distance-decay relationships, taxa-area relationships or local:global taxa richness. And these sources of information often offer mixed, when not contradictory, information about the similarities and differences between microbes and macrobes. The heterogeneity in the sources of evidence and other potential confounding effects such as the spatial scale of the analysis limit the explanatory capacity of the works that try to infer the processes driving the spatial patterns of microorganisms (De Meester, 2011; Hortal, 2011; Jenkins et al., 2011).

4. Empirical evidence

Microscopic organisms encompass almost all major groups of living organisms, as they are defined, for biogeographical purposes, as being smaller than 2 mm. Thus,

prokaryotes and unicellular eukaryotes fall into this group, together with microscopic animals and fungi. Moreover, other groups of organisms, larger in size, have microscopic dispersing stages and, for biogeographical purposes, can be considered in this review, like fungi, lichens, mosses and ferns (Fontaneto, 2011).

4.1 Prokaryotes

Some recent studies on prokaryotes have attempted to address spatial patterns in bacterial and archaeal taxa with respect to spatial scales, environmental factors and temporal scales (Green & Bohannan, 2006; Hughes-Martiny et al., 2006; Prosser et al., 2007; Lacap et al., 2011). The existence of taxon-area relationships, where species richness increases with the amount of area sampled, has been found for tree hole bacteria and salt marsh bacteria (Horner-Devine et al., 2004; Bell et al., 2005). The existence of a distance-decay pattern for soil prokaryotes has been demonstrated on small scales (metres) (Franklin & Mills, 2003), and on larger scales (Cho & Tiedje, 2000; Reche et al., 2005). Other studies have concluded that the influence of environmental heterogeneity was more important than geographic distance as a driving force shaping community composition (Lacap et al., 2011). There are even evidences of ‘ancient endemism’ in prokaryotes (Takacs-Vesbach et al., 2008; Pointing et al., 2010). Thus, even if diversity in prokaryotes is underestimated and range sizes are generally wider than in larger organisms, biogeographical patterns seem to exist, in contrast to the ubiquity hypothesis.

4.2 Unicellular eukaryotes

The main proponents of the ubiquity hypothesis in protists have been Finlay, Fenchel and colleagues (e.g. Finlay et al., 1996; Finlay, 2002; Fenchel & Finlay, 2004; Finlay & Fenchel, 2004). The original formulation of the ubiquity hypothesis for protists uses morphology-based definitions of the taxonomic units (Fenchel & Finlay, 2006). Apart from the problems of such approach discussed above, many protists of different groups are not globally distributed even at the level of morphospecies (Bass & Boenigk, 2011); these groups include unicellular green algae (Coesel & Krienitz, 2008), planktonic foraminifera (Darling & Wade, 2008), testate amoebae (Smith & Wilkinson, 2007; Heger et al., 2011), ciliates (Foissner et al., 2003; Stoeck et al., 2007), diatoms (Vanormelingen et al., 2008), and chrysophytes (Kristiansen, 2008).

Thus, unicellular eukaryotes seem to exhibit a combination of cosmopolitan and restricted distributions, similar to the patterns found in prokaryotes. Even using only a morphological approach in species identification, in his review of the subject Foissner (2011) suggested that the most important factors describing biogeography in protists are the resting cysts and the geological history: that is, a combination of spatial and biological features limiting dispersal capabilities. Further, based on their review of evidence coming from molecular tools, Bass & Boenigk (2011) suggested that “the most sensible view is that protist distribution is not fundamentally different to that of other organisms - the apparent differences being quantitative rather than qualitative”.

4.3 Multicellular eukaryotes

Almost all groups of multicellular microscopic organisms analysed so far show the same trend of prokaryotes and protists, with evidence of both widespread and restricted distributions, most of the time related to biological properties other than size (Artois et al., 2011; Guil, 2001). The few groups analysed at the community level, such as tardigrades and rotifers, also show responses to environmental gradients similar to those of macrobes (Fontaneto & Ricci, 2006; Guil et al., 2009a; Obertegger et al., 2010).

An even stronger biogeographical pattern is present in larger organisms with microscopic dispersing stages, which should in principle allow global distribution, such as fungi (Geml, 2011), lichens (Werth, 2011), mosses (Medina et al., 2011) and ferns (Schaefer, 2011). Thus it is also true for multicellular organisms that being microbial in size or with a microscopic dispersing stage is not the only requisite for cosmopolitan distribution.

5. Consequences and theoretical implications

A general theory of microbial biogeography is yet lacking. However, despite scarce and sparse, the information on the geographical responses of microscopic organisms may be just enough to develop a theoretical framework that will lay the foundations of such theory. Some efforts have been made in that direction (see also Hughes-Martiny et al., 2006; Green & Bohannan, 2006; Telford et al., 2006; Green et al., 2008), but further integrative work is needed to solve some key questions. Perhaps the most important of these questions is whether everything small is everywhere, because it

informs on the spatial dynamics of microbes across scales. It now seems clear that the large dispersal potential of microbes does not necessarily result in high rates of *effective dispersal* (i.e. successful dispersal events, see Weisse, 2008). Due to this, many microscopic organisms do not maintain significant levels of gene flow between geographically remote populations (Bohonak & Jenkins, 2003; Foissner, 2006, 2008; Jenkins et al., 2007; Frahm, 2008; Weisse, 2008). This results in the geographically structured genetic differences (i.e. phylogeographic variations) that have been found for many microbial taxa (e.g., Whitaker et al., 2003; Mills et al., 2007; Prosser et al., 2007; Vos & Velicer, 2008).

Another consequence of the combination of the potential for long-distance dispersal events with limited rates of effective dispersal is the particular scaling of the spatial structure of many microbial distributions. According to De Meester (2011), the geographical distributions of free-living terrestrial microbes are determined by the interplay of processes acting at the metacommunity and biogeographical levels. Within a region, the structure of microbial metacommunities is driven by their high dispersal, typically in a gradient between species sorting and mass effects; here, species sorting occurs when dispersal is sufficient to allow the species to colonize all suitable patches but not so high to allow maintaining populations in unsuitable patches, and mass effects when dispersal is so high that it allows maintaining populations in unsuitable patches through source-sink dynamics, reducing the match between the distribution of species and the composition of communities and the local environmental conditions (see Leibold et al., 2004). Between geographically distant regions, monopolization processes will be most important (De Meester, 2011). Monopolization arises as a result of the combination of high dispersal rates with the high population growth rates, short generation times and capacity to produce dormant stage banks that are typical of many microscopic organisms. The combination of these characteristics may often result in strong numerical advantage of first colonizers, which is maintained thanks to the colonization from the bank of dormant individuals and reinforced by local adaptation, providing the resident population with great advantage over new colonizers (De Meester et al., 2002; Urban & De Meester, 2009). This dual process will produce restrictions to species distributions globally (thus allowing the appearance of endemism and phylogeographic structure), while maintaining widespread distributions regionally. Further, it provides an explanation for the differences in the strength of species replacement between patches of different

habitats found for some microbial groups (e.g. Fontaneto et al., 2006) as well as for the importance of distance in determining such replacement between environmentally different sites (e.g. Verleyen et al., 2009): the similarity in species composition between different habitats will increase depending on how strong mass effects are for the majority of species within the landscape.

Following De Meester's (2011) framework, another major difference between microbes and macrobes lies in the different *magnitude* of the distance-dependent changes in species composition across similar habitats. The much larger distances needed to find similar degrees of compositional changes result in a completely different scaling between the macroecological relationships observed in microbes and macrobes, despite other processes being similar in both groups. A good example is the relationship between diversity and area, one of the most studied relationships in the biogeography of large organisms. The number of species (or any other diversity unit) typically increases with area; the larger the area, the more species are present. This is true for both discrete patches of habitat that differ in area (i.e. larger ones host more species), and for progressively larger portions of an apparently homogeneous territory. While the former mostly relates to the capacity of a territory of hosting more species (i.e. carrying capacity), the latter is due to variations in the species composition of the communities throughout space (see reviews in Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007; Lomolino et al., 2010). Strikingly, currently available evidence indicates that while such spatial replacement in the composition of local communities occurs at much larger scales for microbes than for macrobes (Finlay et al., 1998; Green et al., 2004), the strength of taxa–area relationships for discrete habitat islands is similar in both groups (Bell et al., 2005; van der Gast, 2005; see also Green & Bohannan, 2006; Prosser et al., 2007). This indicates that although the composition of microbial communities changes with distance at a lower rate than macrobes, the restrictions to diversity imposed by area may be similar for both groups of organisms (Hortal, 2011).

Other macroecological relationships well-known for macrobes are also relevant to microbes. The diversity of microbial communities varies along environmental gradients; in particular, altitudinal variations in richness have been found at least for rotifers, tardigrades and bryophytes (Fontaneto & Ricci, 2006; Fontaneto et al., 2006; Guil et al., 2009a; Oliveira et al., 2009; Obertegger et al., 2010). These climate-driven diversity variations in microbes may simply be the result

of species sorting, due to the differences in niche requirements of each of the species regionally available (see above). In fact, in two of the examples given above many species of both bdelloid rotifers and tardigrades show strong habitat selection (i.e. habitat sorting; Fontaneto & Ricci, 2006; Guil et al., 2009b). This is consistent with a high potential for dispersal and local environmental selection, thereby being more likely to occur when many species are closer to species sorting-like metacommunity dynamics in the framework proposed by De Meester (2011). However, the limited information available, which is scattered between empirical and experimental studies of different groups and types of habitats, impedes the formation of a solid conclusion on the mechanisms driving the dependence of microscopic organism diversity on both area and environmental gradients.

Regardless of the origin of geographical gradients, a straightforward consequence of the spatial variations described above is the existence of geographic differences in the ecosystem functions provided by microbial communities. Different aspects of the diversity of microbial communities, from richness to composition or functional structure, affect ecosystem productivity and functioning (Laakso & Setälä, 1999; Fukami & Morin, 2003; Heemsbergen et al., 2004; Sánchez-Moreno et al., 2008). Given the importance of microscopic organisms for performing and/or maintaining many ecosystem services, the geographic variations in microbial diversity will have important functional consequences (Naeslund & Norberg, 2006; Green et al., 2008). However, like many other aspects of microbial biogeography there is as yet little knowledge about the large-scale impacts of these geographic differences in the ecological functions performed by microscopic organisms.

6. Outlook

Although the first observations on the geographical distribution of microscopic organisms date from the Twentieth Century, the discipline of microbial biogeography is still in its infancy. The distributions, genetic structure and community variations in space have been comprehensively studied only since the 1990s; in part thanks to the re-opening of the debate on whether everything small is present everywhere. In spite of the limited amount of information available and its sparse character, evidence points clearly to the existence of biogeographical patterns in microscopic organisms. However, these patterns may be markedly different from those observed for macrobes. These differences are not only generated by their different size, but also by

the basic ecological differences between both types of organisms. In contrast with the majority of large organisms, microbes have a great potential for dispersal; they are able to produce massive numbers of propagules and to disperse long distances passively in dormant stages. This allows them to reach localities placed much farther apart than any macroscopic organism, and at the same time allows colonizing species to monopolize a locality or region by flooding the available habitats with their propagules, thus impeding other species to establish populations. These particularities result in much lower rates of species replacement with distance compared to those observed for macrobes, as well as in higher rates of establishing populations in environmentally suboptimal habitats. But, at the same time, the same processes produce macroecological responses of diversity to area and environmental gradients that are in essence similar to those of macrobes. Further research is yet needed to determine the generality of these processes and the development of a robust body of theory that allows the establishment of microbial biogeography as a mature research field.

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