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PART I

Theoretical framework

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Why biogeography of microorganisms?

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1.1 The problem

The aim of this book is to discuss the idea that for microorganisms 'Everything is everywhere' (EiE hypothesis), that is, large organisms have biogeographies, whereas microscopic ones do not have any large-scale spatial pattern of distribution: microorganisms have no biogeographies.

Size is known to be among the supreme regulators of all biological entities. Shape of any organism is mostly a consequence of its size; how the organism interacts with the environment and all its biological functions are a matter of its size; its life history is influenced by its size (Calder, 1996; Bonner, 2006). The strongest correlate of body size is that body volume and body surface are not linearly related. Thus, larger organisms have different needs from small ones regarding temperature, osmosis, physiology, metabolism and many (if not all) other processes (Schmidt-Nielsen, 1984; Peters, 1986). Body size also determines what an organism may be able to do, even its extinction risk, and the communities and the ecosystems the organisms live and interact in (Colinvaux, 1978; Cardillo and Bromhan, 2001; Hildrew et al., 2007).

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Most of these theories, hypotheses and models attempt to describe some continuous function relating biological patterns and processes with body size, and universal scaling laws in biology have been formulated and tested (Brown and West, 2000). A notable exception to this is the biogeographic implication of body size. Instead of a gradient in the patterns of diversity from large to small organisms, an abrupt distinction has been hypothesised between large and small organisms, with 2 mm being the empirical threshold value discriminating macroorganisms with biogeography and microorganisms without biogeography (Finlay, 2002; Fenchel and Finlay, 2004).

The underlying biological assumption for this abrupt threshold is that microorganisms are really different from macroscopic ones. The threshold dividing these two groups of organisms should fall between 1 and 10 mm, with 2 mm being the most probable size (Fig 1.1). The peculiar features of microorganisms allow them to attain cosmopolitan distribution, an uncommon characteristic in most large organisms: microorganisms are so small that they can be easily passively dispersed everywhere, they produce resting stages that allow them to survive adverse conditions and to persist in any habitat (see Chapter 5 for a detailed report on the effect of resting stages), and can use asexual or parthenogenetic reproduction to quickly increase in number (Shön et al., 2009; see Chapter 15 for a detailed account of the influence of body size, dispersal rate and abundance). However, the hypothesis that for microorganisms everything is everywhere (‘ubiquity hypothesis’) is

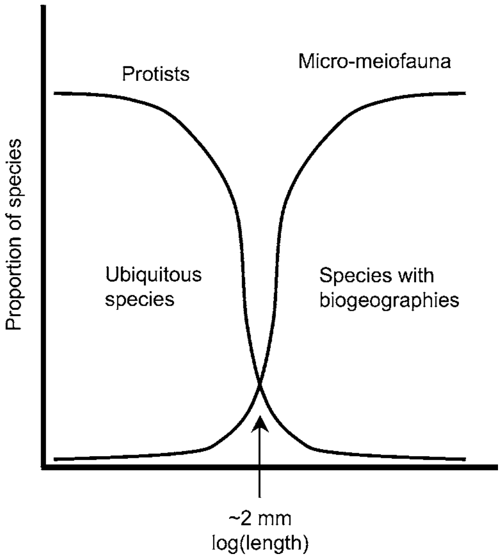

Fig 1.1 Hypothetical model of the transition between larger organisms with biogeography and microscopic organisms without biogeography. Modified from Finlay (2002).

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controversial in the current scientific discussion, and in opposition to the 'moderate endemicity model' by Foissner (1999, 2006), which suggests that many microorganisms have restricted distributions (Chapter 5).

Why is the ubiquity hypothesis for microorganisms controversial? Why are scientists still arguing for or against it? Is there evidence supporting or contrasting it? There are many issues in the EiE hypothesis that will continue to be unresolved for a while. They include, for example, our current inability to reliably describe diversity in microorganisms, to quantify the ecological niche and the geographic range of most species, and to define their rates of dispersal. Moreover, knowing if and how microorganisms attain global distributions is a far-reaching topic. For example, is speciation happening also in the absence of geographic barriers isolating populations? What about environmental conservation? If microorganisms are not linked to any geographic area, how can they be conserved? Here we introduce some of the problems of the biogeography of microorganisms, which will be discussed later in more depth in different chapters.

1.2 Taxonomic units

The current formulations of EiE use morphology to define the taxonomic unit under consideration (Fenchel and Finlay, 2006). Nevertheless, finding reliable morphological taxonomic characters for most microorganisms is notoriously difficult; we need to define unambiguous units of diversity in order to map their distribution. Thus, many species considered cosmopolitan may represent species complexes with restricted distributions. Almost all the chapters in the book discuss this topic, reviewing the current knowledge of species reality and identity in each group, and how new tools can help in providing reliable estimates of diversity. On the one hand, molecular taxonomy helps morphological taxonomy to reveal species complexes and potentially identify the correct units of diversity (e.g. Pons et al., 2006; Burns et al., 2008); on the other hand, environmental sequencing by cloning PCR products but mostly by ultrasequencing, is providing distributional data of many taxa otherwise unrecorded or undistinguished (e.g. Robeson et al., 2009; Creer et al., 2010).

1.3 Niche definition

The complete statement of the ubiquity hypothesis for microorganisms is that 'everything is everywhere, but the environment selects' (Baas Becking, 1934; de Wit and Bouvier, 2006). Thus, knowledge of the ecological niche for these organisms ('the environment selects' part of the hypothesis) is needed in order to define their distribution, and niche-based models are used for predicting biogeographic

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distributions (see Chapter 15). But this is far from reality, because the identification of ecological needs for microorganisms may not be as straightforward as for larger organisms. This is partly due to technical difficulties in measuring environmental parameters at the microscopic scale, but also to the fact that the presence of microorganisms in an area does not mean that the environment is suitable. A detailed example is given in Chapter 4, reporting on thermophilic bacteria in cool soils. This aspect will not be improved by the recent advances in environmental sequencing with ultrasequencing (e.g. Creer et al., 2010), as the results of such analyses will show species even in habitats where they do not live but where they are only present as resting stages.

1.4 Spatial patterns

Reports on findings of species and species lists are the basis for any biogeographic analysis. For microorganisms we already know that there are many problems in identifying ‘species’ as units of diversity. In this case, new advances in molecular tools will provide more reliable data on the geographic distribution of microorganisms.

Nevertheless, following from the problem of defining ecological niches for these organisms, it will also be difficult to disentangle the contribution of historical vs. ecological biogeography. The difference between historical and ecological biogeography and the implications for the study of the distribution of microorganisms are explained in detail for protists in Chapter 6 (section 6.2): large organisms usually have very small discrepancies between their potential, historically derived biogeographic range and their realised, ecologically derived ranges, whereas microorganisms, due to their resting stages, may be present in areas that are not ecologically optimal for them (Chapter 4). The difference between historical and ecological biogeography highlights one of the major differences in dispersal between micro- and macroorganisms, and one of the difficulties in supporting or falsifying the EiE hypothesis.

To further complicate the scenario, the various chapters on the biogeography of all the microorganisms report both evidence of large distributions and of endemic, restricted distributions. Phylogeographic analyses, using DNA sequences to investigate the spatial patterns of distribution are conveying similar results, providing evidence of both long-distance gene flow and restricted gene flow.

Moreover, the spatial scale of the analysis, the measurement used (distance–decay relationships, taxa–area relationships, local:global taxa richness), and other potential confounding effects may become important when trying to infer the processes driving the spatial patterns (Chapters 15–17).

1.5 The challenge

To take up the challenge of the biogeography of microorganisms, this book brings together empirical observations of the patterns in different groups of microscopic organisms or with microscopic dispersing stages. Different approaches are used in the description of diversity in order to support or not the hypothesis of cosmopolitanism for microorganisms. Moreover, the book goes a step further and discusses the processes and the generalities obtained from these examples. The main result is that in all the groups, evidence of restricted distribution is more common than generally accepted. Thus, the differences between micro- and macroorganisms may not be so strong.

The book is divided into five main parts. The first part (Chapters 1 and 2) provides a brief introduction and an historical and philosophical overview. The following three parts deal with the empirical evidence gathered in different microorganisms, from prokaryotes (Part II, Chapters 3 and 4), to unicellular eukaryotes (Part III, Chapters 5–8), and pluricellular eukaryotes (Part IV, Chapters 9–14). Finally, the last part focuses on the processes and the generalities in the biological properties of microorganisms (Chapters 15–17). The subdivision in different parts serves more as a structure for the book than as a logical continuum. Each chapter can be read alone, as it contains an overview of the problem, empirical evidence and a discussion of the processes. The focus is different in different parts: chapters in Parts II–IV deal with taxon-based evidence and mechanisms, whereas the chapters in Part V are not taxon related, but more mechanism related. So, every chapter presents its own view on the biogeography of microorganisms, providing a theoretical framework, explaining problems and suggesting ways to solve them.

Chapter 2 deals with an historical introduction of the origin of the hypothesis that everything is everywhere, from the first studies at the beginning of the twentieth century; it provides a philosophical background for the hypothesis; it discusses the role of classification of taxa and areas, and then uses the diatoms as an example.

Part II deals with the biogeography of the smallest of all living organisms, prokaryotes. Chapter 3 provides a general review of the current knowledge of prokaryotic biogeography, discussing also problematic topics such as species concepts and identification in prokaryotes, and estimates of diversity. The following chapter (Chapter 4) describes a specific example of thermophilic bacteria in cool temperate areas. It provides also tests on the potential activity of these organisms in a potentially unsuitable habitat and a discussion on mechanisms of transport and the potential sources.

Part III deals with unicellular eukaryotes (protists and yeast); two of the chapters provide general reviews using data from morphological taxonomy

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(Chapter 5) and from phylogenetic and phylogeographic analyses (Chapter 6); one reports on the example of testate amoebae (Chapter 7); and one on the example of cactophilic yeast (Chapter 8). Chapter 5 starts by assuming that the moderate endemicity model is a better explanation for the evidence, and then pays attention to the reasons why certain species are cosmopolitan and others are not. The most important factors described in Chapter 5 are resting cysts, geological history and human introductions. The chapter provides a detailed report of the biogeography of many species to support its initial assumptions. Chapter 6 adopts a different approach dealing with the same organisms, free-living protists. It reassesses the fundamental principles behind the EiE concept in the light of recent findings and insights from twenty-first century molecular biology and microbial ecology. The chapter also discusses the implications of species concepts and identification, estimates of diversity, evidence for biogeography and the differences between historical and ecological processes in biogeography. Chapter 7 describes the example of Arcellinida testate amoebae, providing evidence of restricted distributions and endemicity in a group of flagship organisms: species so charismatic and easy to recognise, whose lack of records in certain areas cannot be attributed to lack of research, but to their actual absence. Chapter 8 deals with yeast, a group of fungi that adopted unicellular growth: these organisms are thus included in the section on unicellular eukaryotes. The yeast example in the chapter is a special one, as it lives in symbiosis with cacti. Thus, it provides a different approach to the problem, discussing the generalities and the peculiarities of the spatial patterns of the system.

Part IV contains six chapters dealing with the biogeography of microscopic pluricellular organisms or of larger organisms with microscopic dispersing stages, such as fungi (Chapter 9), lichens (Chapter 10), mosses (Chapter 11), ferns (Chapter 12) and animals (Chapters 13 and 14). Chapter 9 deals with genetic evidence of patterns of intercontinental gene flow in arctic-alpine and boreal-temperate macroscopic fungi, which have single-celled microscopic dispersing spores. Chapter 10 deals with the biogeography of lichens, providing evidence of wide, disjunct and endemic distributions, focusing mostly on the fungus symbiont; moreover, it reports the little evidence available at present for the biogeography of the algal symbiont. Chapter 11 discusses the biogeography of mosses. These plants are macroscopic, but they all have microscopic dispersing spores. As in the previous chapter, there are records of wide, disjunct and endemic distributions, and of both spatially restricted and not-restricted gene flow. Chapter 12 takes a different approach, dealing with ferns. These plants also have microscopic dispersing spores. The chapter deals with chorological and phylogeographic analyses, trying to disentangle whether dispersal limitation or habitat quality shapes the distribution ranges of ferns. Chapter 13 focuses on microscopic animals, which have dormant stages that can act as dispersing propagules. It gathers empirical evidence on a wide range of groups from a morphological perspective in species identification, showing that the biological peculiarities of the taxa are more important than size alone. Chapter 14 deals with the same groups of microscopic animals, but using recently published evidence from molecular taxonomy and phylogeography. The results are qualitatively similar, with evidence of both widespread and restricted distributions.

Part V has three chapters focusing on the processes and on the biological properties of microorganisms. Chapter 15 uses microorganisms to test the generalities of biogeographic principles. It deals with the effect of abundance, body size and niche constraints on the spatial patterns of distribution. Chapter 16 provides a metacommunity perspective, dealing with species sorting, mass effects, patch dynamics and the neutral model. Chapter 17 analyses geographic gradients, suggesting that microorganisms may not be so different from macroscopic ones, and provides a rationale for the use of microorganisms in what can be called 'experimental biogeography'.

1.6 Conclusions

As a summary of the ideas expressed in the chapters of this book some main conclusions arise: several distribution patterns are described and different processes are hypothesised to explain them. Long-distance dispersal is evidently possible, but it is not the rule, as other distribution patterns can be explained by other mechanisms, such as continental drift, stepping-stone migration and anthropogenic introduction.

The EiE hypothesis focuses on one single explanatory factor, dividing organisms into two main groups, larger organisms with biogeography and smaller ones without biogeography. Given the complexity of the spatial patterns in microorganisms, it seems that their biogeography is more likely to depend on a complex set of interacting phenomena, in which size is of course important, but it is not the only driver. The differences between micro- and macroorganisms can thus be included in a gradient, disregarding the hypothesised abrupt threshold assumed by the EiE hypothesis.

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2

Historical biogeography, microbial endemism and the role of classification: everything is endemic

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2.1 Introduction

Microbial biogeography, the study of the distribution of 'small' organisms, has been said to have gained renewed vigour because of the recently resurrected 'Everything is everywhere' hypothesis (EiE) (Finlay, 2002; Fenchel and Finlay 2003; Finlay and Esteban, 2007). That hypothesis was concisely summarised by the organisers of the conference on the biogeography of microorganisms in Leiden, August 2009, in the promotional material:

> This symposium is based around the hypothesis of everything-is-everywhere (EiE) amongst small organisms. This hypothesis was proposed at the beginning of the twentieth century for microbial diversity and, about ten years ago, extended to describe spatial patterns of diversity for any organism smaller than two mm, under the simple observation that microscopic organisms such as protists seem to be cosmopolitan, at least in habitats that support their growth. Since its recent resurgence, this topic became hotly debated, with evidence apparently supporting and denying the hypothesis.

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