Chapter 1
The Microbiological Promises of Extreme Soils

Patrice Dion

1.1 Introduction

Whereas the notion of extreme environment has received much attention from microbiologists, this generalization does not systematically include extreme soils. There may be at least two reasons for this. First, any soil may be considered as extreme for the colonizing microbes constantly facing starvation, desiccation, predation, and other attacks. In this sense, the notion of "extreme soil" would appear pleonastic. A second reason for the uncommon use of the term "extreme soil" might be the opinion that there is little to be gained from it, inasmuch as every soil has its particularities and, in its very nature, is refractory to human efforts at unification and simplification. In this sense, any grouping of soils from, say, the Antarctic or hot deserts into a common category designated as "extreme" would appear futile, if not detrimental to a precise understanding of soils and their microbial populations. However, one might take the stance that, although it certainly serves to be aware of these difficulties, there is still much to be learned from running into them. Hence, it is hoped that the present book will be a demonstration of the usefulness of the extreme soil concept to microbiologists.

Various extreme soils have been the topic of numerous and fruitful studies dealing with the characterization of microbial communities and processes. These studies have done much to enrich our understanding of microbial diversity and of biogeochemical and other biological mechanisms. They allow us to grasp microbial adaptability and to envision practical applications. Reading the enclosed collection of chapters will make it clear that unifying these studies under the general theme of "extreme soils," and associating this concept with the broader notion of "extreme environments" leads to essential theoretical and practical advances.

We qualify a soil as "extreme" when it supports colonization by organisms presenting a specific and common adaptation. The specifying character of an extreme soil may be physical in nature, and correspond to extreme values of temperature, or

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P. Dion and C.S. Nautiyal (eds.), *Microbiology of Extreme Soils*. *Soil Biology 13*

to exposure to radiation or intense heat. Alternatively, it may also be defined in chemical terms, with the salt content or the presence of toxic pollutants exerting a preponderant influence on microbial processes. The extreme character may be conferred on soils by climatic, geological, or other environmental factors, or else by human activities. One might observe here that the distinction between nature-driven and anthropogenic processes is becoming increasingly blurred, as a result of our improved capacity to relate effects to their cause, and also as human activities exert an ever stronger influence on an expanding scale.

The chapters included in this book provide a careful description of microbial communities exposed to various soil-borne challenges. Bringing together analyses of a wide range of soil systems invites comparative assessments and well-founded extrapolations. Thus, it is hoped that, in addition to providing timely knowledge about extreme soil microbial dwellers, the book will pay tribute to a vast and largely unexplored territory wide open to microbiological enquiry. Indeed, extreme soils promise crucial progress in our understanding of microbial activities and adaptation processes, as well as in our ability to rationally influence ecosystems upon which terrestrial life depends.

1.2 Extreme Soils and Microbial Community Structure and Evolution

Following an unprecedented search for marine microbial sequences, an immense diversity of marine bacteria was revealed, with at least 25,000 different types of micro-organisms being estimated to exist per litre of seawater. The methods used in the study made it possible to relate intraribotype genetic variation to environmental factors. Species may be organized into subtypes, and the corresponding variation results from physical barriers, short-term stochastic effects, and functional differentiation acting in combination (Rusch et al. 2007). Comparison of marine and terrestrial organisms showed that 68% of the nearly 7,000 examined protein domains varied between the two classes of micro-organisms, this variation being in part the result of different metabolic requirements for marine and terrestrial life (Yooseph et al. 2007). These results are a testimony to adaptability of microbial life.

Extreme soils offer us an opportunity to understand microbial diversity as an adaptive response that both reflects and multiplies environmental diversity. Indeed, the soil can be hot or cold, acidic or basic, wet or dry, saline, radioactive, polluted with heavy metals or hydrocarbons, or located on Earth or some other celestial body. Soil microbes pay tribute to this multiplicity of characters by undergoing and maintaining diversification (see Chapter 2).

Extreme environments present peculiar evolutionary challenges to prokaryotes, to which might correspond peculiar evolutionary responses. Identification of these specificities may reveal hitherto unnoticed aspects of evolutionary processes. In particular, extreme conditions might force evolution of traits that are otherwise invariant. More generally, studies on extremophile evolution may help shed light on the roles of environmental pressure in driving evolution. Indeed, competition between individuals may play a larger role in nonextreme environments, whereas environmental pressures would be determinant under extreme conditions. Soils are physically constituted by the orderly collection of sizable and interacting structures. Physicochemical parameters are superimposed on this primary framework. Microbial niches and corresponding diversity are defined by a series of combinatorial operations that the various organizational levels of the soils render possible (see Chapter 3).

In comparing microbial communities of nonextreme and extreme soils, it becomes apparent that extreme soil communities reach unique equilibria, corresponding to under- or overrepresentation of certain community components. The degree to which community member exclusions and inclusions occur, and the nature of these processes, vary in different extreme soils. Attempting a synthesis of these particular responses may lead to identification of crucial microbial mechanisms for survival, growth, dissemination, and adaptation. Such a synthesis may also provide insights on the forces at play to shape and structure biological communities in extreme as well as nonextreme soils (see Chapter 4). Biogeochemical cycles, as they operate under extreme conditions, bring into sharp focus important aspects of microbial community functioning and bear direct relevance to global equilibria (see Chapters 7, 9, and 14).

1.3 Extreme Soils and Microbial Physiology

Comparisons of microbial adaptations in extreme soils and other extreme environments suggest commonalities in physiological processes and cell adaptations. For example, patterns of adaptation to heat and cold, through adjustments in protein thermal stability and membrane composition (see Chapters 2, 3, and 8), are similar in extreme soils as in other environments. Also, compatible solutes contribute to maintain osmotic balance in halophilic organisms from saline soils and other saline environments (see Chapter 5). Such a pattern of common adaptations, superimposed on additional and specific adaptations to soil, water, or other environments, is suggestive of modularity in microbial evolutionary processes. Modules can be defined as "building blocks of interacting elements that operate in an integrated and relatively autonomous manner" (Schlosser 2004). Modules may be thought of as structures, but also as processes, that would be articulated according to three principles. These principles are: (1) connectivity, meaning that they are triggered in a switchlike fashion by a variety of inputs; (2) hierarchization, implying that modules may be spatiotemporally embedded in higher-order modules, or overlap by sharing common elements; and (3) multiple instantiation, which contributes to delimitate a module from others of the same type by its independent perturbability during development. Specifically, modules of evolution are units of integrated and context-insensitive evolutionary changes (Schlosser 2004). From these considerations, it appears that adaptive processes in extreme soil bacteria may be modular, in the sense that adaptations to the soil and extreme components of the environment may occur somewhat independently, while influencing each other through epistasis (see Chapter 3).

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http://www.springer.com/978-3-540-74230-2

Microbiology of Extreme Soils
Dion, P.; Nautiyal, C.S. (Eds.)
2008, XVII, 369 p., Hardcover
ISBN: 978-3-540-74230-2