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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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).

It might be worth mentioning in this respect that relatively little is known on physiology of life in arid environments and the adaptations involved. In most studies, water stress refers to external solute excess, rather than dehydration. Whereas salt and water stress often come together (Wierzchos et al. 2006), and may be both dealt with through osmotic adjustment (see Chapter 2), it is possible to distinguish between tolerance to salt and to water in plants (Munns 2002), and also perhaps in micro-organisms (Zahran 1999). Most studies where dehydration is considered refer to food (Grant 2004). Studies on arid soils deal mainly with community structure (McKay et al. 2003; see also Chapter 6) and little is known about microbial physiology and adaptations, as many of the dominant organisms in arid soils yet remain to be isolated (Drees et al. 2006). One aspect that is being studied is the physiology of photosynthesis in cyanobacteria colonizing arid soils (Lüttge et al. 1995; Ohad et al. 2005). It is also known that, in *Deinococcus radiodurans*, radiation and desiccation resistance are correlated (Mattimore and Battista 1996), and related at least in part to a remarkable capacity for reassembly of broken chromosomes (Zahradka et al. 2006).

1.4 Microbial Functions in Extreme Soils

Modularity, which occurs at the level of cell adaptation to the extreme and soil environmental components, may also be identified as a defining factor of soil microbial communities, where it arises as a consequence of redundancy and complementarity of soil functions (Nannipieri et al. 2003). Redundancy allows microbial groups to be considered as equivalent and interchangeable with respect to function, thus buffering biogeochemical cycling and other ecosystem processes against restricting changes, such as selection and metabolic tradeoffs.

The extreme character acts on redundancy, diminishing it without altering ecosystem processes (see Chapter 4). This results in a strengthening of the correspondence between identity and function, and leads to a better illustration of microbial function as it more directly relates to particular microbial types. Clues to this simplifying, looking-glass effect are proposed in this volume, and are provided, for example, by observations on dissimilatory sulfate reduction by certain halophiles in saline soils and their role in ecosystem functioning (see Chapter 5), hydrocarbon degradation as it is performed by permafrost microbial communities (see Chapter 12), and involvement of endo- and ecto-mycorrhizae in radionuclide uptake and transfer to plants (see Chapter 16). It may well be that further studies on these and other systems will highlight the potential of extreme soils as simplified objects for study of microbial processes.

1.5 Practical Value of Extreme Soils

Like a cat, the Earth cleans itself continuously, although there is growing concern that autogenous processes may not suffice given the extent of human-inflicted damage. Soil contamination occurs worldwide, and it is striking that bacteria from pristine Arctic soils express *mer* (or mercury resistance) genes (Poulain et al. 2007).

One might consider the degradation or elimination of pollutants as yet another manifestation of overall soil productivity, and then be led to suggest that the intrinsic cleanup potential will be less in extreme soils, as compared to nonextreme soils. This suggestion arises from the conjunction of two observations, which are, first, that microbial diversity is often lower in extreme soils than in nonextreme soils (see Chapter 2), and, second, that ecosystem productivity increases with biodiversity (Tilman 1999). On the other hand, extreme soils might be more responsive than nonextreme soils to application of exogenous microbial inoculant with remediating activity, as lower diversity might make communities more susceptible to invasions (Tilman 1999).

The relationship between diversity and stability of an ecosystem is the object of some controversy and may be influenced by species composition (Bezemer and van der Putten 2007; Tilman et al. 2007). This may explain why attempts at accelerating the degradation of oil pollutants in Antarctic soils through bioaugmentation are often unsuccessful (see Chapter 12).

Conceptually, two situations may arise, with the extreme soil parameter being the direct object of the bioremediation process or simply acting as an intrinsic confounding factor. Attempts to use bacteria to reduce the impact of salts (Bacilio et al. 2004; Ashraf et al. 2006) or heavy metals (see Chapter 15), belong to the first category, and, in this case, the extreme character of the soil will become attenuated following successful treatment. Bioremediation efforts of hydrocarbon-contaminated cold (see Chapter 12) or arid (see Chapter 13) soils fall into the second class of bioremediation interventions.

Extremophiles offer an ever-expanding domain to biotechnological applications (Podar and Reysenbach 2006), and extreme soils represent a rich and still relatively unexplored source of useful microbes. For example, halophiles colonizing saline soils produce a wealth of macromolecules and small compounds of potential use (see Chapter 5).

1.6 Extreme Soils and the Boundaries of Life

Although there are sound and totally unemotional reasons to send humans into space instead of strictly relying on robots (Crawford 2004), the fascination exerted by human expansion through the Earth and beyond points to additional motivations. In yielding to our relentless drive to expand, we are doing little more than applying virtually unlimited imagination and technical skills to satisfy our innate desire at self-perpetuation. Along the process, and especially since the end of the Cold War, we are conducted to establish the pacifying image of humanity as a constant creator of knowledge and settings. Not surprisingly then, life as it is envisioned elsewhere in the cosmos is often portrayed as akin to Earthly biological processes (Pace 2001), which is certainly a reasonable view as long as we restrict our exploratory range to our immediate planetary neighbors. Looking farther beyond, a variety of other chemistries based on liquids other than water may be envisioned (Bains 2004; Benner et al. 2004).

Following its formation 4.6 billion years ago and early bombardment, Mars is believed to have been through three geologic ages, the first of which, termed the phyllosian era, coincided with a nonacidic aqueous alteration of planetary material. The planet might have been habitable during this period, which ended 3.5 billion years ago, when surface water became increasingly acidic during the theiikian era, and then disappeared to initiate the siderikian era, that is still going on today (Bibring et al. 2006). However, liquid water might have resided very close to the surface throughout Mars' history, as is indicated by the observation of gullies filled during the last decade with a liquid that might be water (Malin et al. 2006). These observations leave open the possibility that Martian life, if indeed it was initiated during the Earth-like phyllosian era, might have been maintained in isolated subterranean oases up to this day (see Chapter 11).

The eventual demonstration and examination of extraterrestrial life will have an unimaginable impact on human thinking. It appears, however, that the mere search for this life is already bearing fruit. It leads us to systematically consider how life can be recognized and studied (see Chapter 11). It provides an incentive to investigate Mars-like ecosystems of our planet, such as sun-bathed deserts (see Chapter 6) or rocks where metabolic energy is extracted from metal chemistry (see Chapter 10). It also leads us to reflect upon and better comprehend ecological processes upon which our lives immediately depend (Wilkinson 2003). Ultimately, we are presented with pictures of our past and our future (see Sections 1.7 and 1.8) and, consequently, our very nature.

While reflecting on the nature of life, Erwin Schrödinger wrote: “Living matter, while not eluding the ‘laws of physics’ as established up to date, is likely to involve ‘other laws of physics’ hitherto unknown, which, however, once they have been revealed, will form just as integral a part of this science as the former” (Schrödinger 1944). Although this view has been amply commented and criticized (Sarkar 1991), it may retain some intuitive value, in the sense that we have entrenched the notion that our current physical knowledge does not fully account for life, even as we know it in its most current manifestations. The history of biological enquiry may be viewed as an endless tentative to restrict and even contradict this notion of life as escaping common physical laws.

Today, we maintain a desire to define life from the outside, that is, to determine where life can and cannot exist and then identify absolute differences between these two classes of environments. Certainly, extremely arid (see Chapters 6 and 13) or cold (see Chapters 7 and 12) land may be viewed as a patchwork of life-prone and life-hostile zones, as does extraterrestrial soil (see Chapter 11). For its part, isolation might not impede life development itself, but rather narrow its manifestations (see Chapter 8). In gaining such a subtractive vision of life, in the sense of determining where life cannot be and what factors restrict its range, we demonstrate the limitations of biological processes and adaptations. Thus, a frontier is drawn, within which life is thought to remain. Within this frontier composed of water and carbon, every known life-related phenomenon exists, from the citric acid cycle to consciousness. However, lingering questions remain: can this frontier be pushed just a bit further? Is there really nothing living beyond it?

1.7 Extreme Soils and Our Past

Inspired by Beijerinck, Bass Becking has said that "Everything is everywhere, but the environment selects," and this statement has been the object of numerous comments (de Wit and Bouvier 2006). Certainly, some observations reported in this book, for example, on the presence of thermophilic endospore formers in cold soils and even Arctic ice (see Chapter 8), or of *Rhodococcus* strains with a capacity for hydrocarbon degradation in pristine Antarctic soils (see Chapter 12) seem to corroborate the notion of a universally shared microbial substratum for environmental selection. However, upon further consideration of this notion, two questions arise, which concern the nature of, first, the environmental selection implied in the statement from Bass Becking, and, second, the mechanisms that have allowed "everything" to have become present "everywhere."

With respect to the first question, bacterial dispersal is likely to set the table for what has been termed "postimmigration evolution" (Novak 2007), that implies that selection of invasive species is accompanied by adaptive genotypic modifications. Furthermore, it appears that these two recognized components of evolutionary processes, mutation and selection, are functionally related and environmentally determined, albeit to various extents. The mutation rate is influenced by various environmental components in addition to classical mutagens, this influence being exerted in the absence of any directionality to mutation events (see Chapter 3). Bacteria take different avenues towards genetic changes, that include horizontal gene transfer in addition to mutation. The ability to acquire foreign genes may itself be influenced by environmental parameters. This may occur indirectly, through the creation of hotspots of high bacterial density where plasmid transfer occurs at increased frequency (Sørensen et al. 2005), or even directly, by SOS-mediated enhancement of expression of genes involved in DNA transfer (Beaber et al. 2004).

Dispersal, that may occur over considerable distances, comes immediately to mind as a possible explanation for the apparent ubiquity of bacteria. However, the notion of bacterial ubiquity must be put in perspective. Some bacterial species, including various plant and animal pathogens, are distributed worldwide, whereas others are endemic. Within cosmopolitan species, some particular genotypes may in fact be endemic. The ability for dispersal would be associated with the presence of particular genes (Ramette and Tiedje 2007a). Reflecting this variation in distribution range, bacterial populations exhibit clear spatial patterns that arise both from environmental heterogeneity and from spatial distance taken as a measure of past historical events and disturbances. Within-species diversity may be influenced by spatial distance as well as by environmental heterogeneity, whereas species abundance and the composition of communities are more influenced by local environmental interactions. However, a considerable proportion of bacterial diversity remains unexplained by the currently measured variables (Ramette and Tiedje 2007b). Because they represent well-defined and localized environments, extreme soils may prove valuable objects of study in bacterial biogeography. For example, suitable and unsuitable habitats for extant soil communities in the Antarctic Dry Valleys are defined by a combination of factors that include current and historical elements. Among the latter are past climates, which influence the level of lakes and glaciers. Also of relevance are legacies of productivity from past ecosystems that influence the chemistry of contemporary soils and their organic matter (Virginia and Wall 1999; see also Chapter 4).

1.8 Extreme Soils and Our Future

Very few areas of our planet now escape human influence, and the global environment may be described as the "human-made context of our lives" (Dalby 2002). Nearly half of the land surface has been transformed by direct human action (Steffen et al. 2004), and sometimes humans may cause catastrophic soil changes that extend over considerable time and space scales. The great Centralia coal fire and other similar events are a case in point, and have considerable impact on soil microflora and other soil properties (see Chapter 14). Indirect human action, particularly through global climate change and what has been termed "global distillation" (or the spread of persistent organic pollutants) may be even more pervasive, with the result that virtually no pristine land is said to remain (Dalby 2002). Thus, we may be experiencing a global extremization of the soils (see Chapter 4), which may affect interactions between humans and a variety of soil-dependent or soil-residing organisms, would these particular organisms be sources of food or disease.

Throughout its modern history, humankind has been able to escape the consequences of its actions by exporting, either its waste or its populations themselves, some less fortunate human groups occasionally suffering in the process as unwilling recipients. Now we have reached a point where these movements appear useless, with a radical transformation of air, water, and soil threatening the self-maintained balance upon which all life forms depend. Particularly worrisome is the spectre of a spiralling uncontrollable process, whereby environmental change becomes the trigger of ever greater and more damaging changes. Such self-sustained processes may eventually occur in peatlands, which have been acting as net carbon sinks and methane sources since the early Holocene. Desiccation of Siberian peatlands would elevate CO_2 concentrations through peat oxidation but would reduce CH_4 emissions, with the outcome on net radiative balance being difficult to estimate. However, the balance may well tilt towards an intensification of greenhouse warming (Smith et al. 2004). This is one reason why microbial communities and processes of peatlands deserve special scrutiny (see Chapter 9). Permafrost soils, where carbon storage and methanogenesis also exist, are similarly preoccupying (see Chapter 7).

Industrialized societies have been especially good at minimizing the impact of microbial pathogens, through a combination of sanitation and hygiene measures, large-scale vaccination strategies, and heavy antibiotic use. Now there are indications that this relatively disease-free era may be coming to an end. Global changes are expected to play a role in this resurgence of microbial pathogenicity, with the poorest nations being hit first and strongest. Soils are well-known reservoirs of microbial human pathogens (Santamaría and Toranzos 2003), so that soil changes may well be associated with modifications in transmissibility and incidences of various diseases.

Many of these changes as they relate to disease transmission concern dispersal. A striking example is provided by Vozrozhdeniye Island, which was once in the middle of the now drying Aral Sea, and hosted the main Soviet center for testing biological weapons, antidotes, and vaccines. Upon shutdown of the Soviet program in 1988, slurries of anthrax spores and other pathogens were buried on the island. Vozrozhdeniye has now grown from a 33-km island to a 145-km peninsula, and, with some of the anthrax spores having remained viable (Whish-Wilson 2002), has become the object of intense surveillance and decontamination programs. In addition to persisting anthrax, a military-grade, antibiotic-resistant strain of plague bacterium may also have survived among the rodent population in the testing range (Pala 2005). There is a possibility of short-term survival of *Yersinia pestis* in soils, embedded in flea feces or tissues of dead animals, and even of its persistence in soils in dormant form or as an intracellular parasite of soil protozoa (Gage and Kosoy 2005).

The recent reconstruction of the 1918 Spanish flu epidemic virus, from the body of a flu victim buried in Alaskan permafrost (Tumpey et al. 2005), should also provide us with an opportunity to ponder the infectious potential of currently inaccessible or inert material. Although not documented still, the possibility exists that seemingly vanished pathogens, including the smallpox virus (Stone 2002), remain preserved in frozen state in permafrost burial sites. Hence, it appears that the study of permafrost-inhabiting microbial communities (see Chapters 7 and 12), while providing a remarkable insight into microbial adaptations and processes, may take unexpected relevance and offer twist endings. The possibility that some Archaea may be as of yet unrecognized human pathogens (Eckburg et al. 2003) also places soil microbial reservoirs and soil changes into a new perspective.

Cioran tells us of Socrates, who, the day before he would die, was learning a tune on the flute. Being asked what good it would do to him, he answered “To know this tune before I die.” Following the philosopher’s example, we will continue learning about extreme soils and their microbial inhabitants. This will help us monitor the changes ahead. We will also be in a better position to cope with these changes, which it is hoped will not prove as dreadful as a cup of hemlock tea.

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