

Microbiology of hyper-arid environments: recent insights from the Atacama Desert, Chile

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Abstract Interests in the Atacama Desert of northern Chile until very recently were founded on its mineral resources, notably nitrate, copper, lithium and boron. Now this vast desert, the oldest and most arid on Earth, is revealing a microbial diversity that was unimagined even a decade or so ago; indeed the extreme hyper-arid core of the Desert was considered previously to be completely devoid of life. In this Perspective article we highlight pioneering research that, to the contrary, establishes the Atacama as a combination of rich microbial habitats including bacteria that influence biogeochemical transformations in the desert and others that are propitious sources of novel natural products. Many of the Atacama's habitats are especially rich in actinobacteria, not necessarily as dense populations but extensive in taxonomic diversity and capacities to synthesize novel secondary metabolites. Among the latter, compounds have been characterized that express a range of antibiotic, anti-cancer and anti-inflammatory properties to which a variety of bioinformatics and metabolic

engineering tools are being applied in order to enhance potencies and productivities. Unquestionably the Atacama Desert is a *living* desert with regard to which future microbiology and biotechnology research presents exciting opportunities.

Keywords Atacama Desert · Bioactive metabolites · Geology · Hyper-aridity · Microbial diversity · Subsurface communities

Introduction: The Atacama Desert

Although the microbiology of extreme environments has progressed substantially over the past two decades, Stephen Jay Gould's observation remains pertinent: 'Bacteria dwell in virtually every spot that can sustain any form of life. And we have underestimated their global number because we, as members of a kingdom far more restricted in potential habitation, never appreciated the full range of places that might be searched' (Gould 1996). Thus, to date, emphasis has been placed largely but not exclusively on deep seas, and hyper-thermal or permanently cold ecosystems (Horikoshi et al. 2011) and the recent description of bacterial communities in the extreme cryogenic brine of Antarctic's Lake Vida (Murray et al. 2012) is a dramatic current example of such curiosity. However, interest in hyper-arid desert

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ecosystems has developed more recently so that knowledge of their microbiology is patchy and overall not well defined; this Perspective while focused on the Atacama Desert has a wider frame of reference for comparable environments subject to extreme hyper aridity. The *raison d'être* for studying microorganisms of extreme environments is several-fold including their biodiversity, ecology (particularly adaptive mechanisms), and biotechnological potential. A workshop convened at the University of Chile, Santiago in October 2012 provided a microbiological overview of Chile's Atacama Desert and in part posited the hypothesis that extreme environments are likely to contain novel microorganisms that express novel chemistry, some of which have new biological activities and hence present putative drug leads.

The Atacama Desert of northern Chile is the oldest and driest desert on Earth having evolved over 100 My of aridity and 10–15 My of hyper-aridity (Gómez-Silva et al. 2008). The mean annual rainfall at the extreme hyper-arid core (the Yungay region) of this temperate desert is no more than 2 mm while long sequences of years have experienced no precipitation. Other regions of the Desert are characterized by extensive salt-pans (e.g. Salar de Atacama) some of which encompass lagoons of variable brine compositions, or are bounded by *altiplano* (e.g. Puna de Atacama). The availability of liquid water and high solar irradiance are generally acknowledged to be the major environmental factors controlling microbial colonization in the Atacama Desert. Coupled with very low concentrations of organic carbon, very sparse or zero microbial population densities and a high oxidizing capacity, these properties have promoted the Atacama Desert as an accurate analogue of Martian soils. Concerted research on the detection and description of microorganisms in Atacama environments go back little more than a decade and are due principally to scientists from universities in Antofagasta (a coastal, copper exporting city and important portal to the Atacama Desert) and US astrobiologists (Navarro-Gonzalez et al. 2003). The Workshop, one outcome of a current project promoted by The Royal Society of London, sought to bring together Chilean and UK microbiologists, chemists, geologists and engineers whose programs focused on the Atacama Desert with the objects of sharing data and expertise, and encouraging both national and international collaborations. Three inter-related themes were discussed at the

Workshop: (1) aspects of the geology, hydrochemistry and soil humidification in salar and extreme hyper-arid regions of the Desert; (2) the microbial diversity of a spectrum of Atacama habitats, including the most recent exploration of subsurface communities, and early attempts to understand functional ecology; and (3) natural product chemistry of Atacama bacteria (with emphasis on actinobacteria and exploitable bioactivities), and the application of systems biology and metabolic engineering techniques to define and modulate product biosynthesis.

Geology and humidity

The Salar de Atacama is a massive compressional basin enclosed between the Cordillera de Domeyko to the west and the Andes to the east, the complex geochemistry of which was discussed by Andrés Fock, Rodrigo Rauld and colleagues from Xterrae Geología, Santiago. The salar is fed from small inflowing rivers out of the Andes but the only outlet from the basin results from the very high evaporation rates. Deposition of salts occurs in order of their solubility within the nucleus of the salar composed of halite (sodium chloride), which is surrounded by gypsum and carbonates. The thick encrustations of these salts has an immediate and dramatic impact on the observer. A particular feature of the inflowing rivers is their different hydrochemical signatures, most notably their concentrations of boron and lithium salts that may arise from the leaching of volcanic rocks and/or hydrothermal action in the cordillera. In a complementary paper Luis Cáceres and Jessica Saldivia (Universidad de Antofagasta) emphasized that rainfall was a very rare phenomenon in the Atacama Desert (only seven alluvial events are on record in the past 100 years), and that fog was the most important source of water for plants and microbial crusts in this environment. The creation of fog depends upon available atmospheric moisture and daily fluctuations in temperature and relative humidity; consequently an understanding of climatic patterns is essential to interpret its occurrence and distribution. Cáceres and Saldivia recorded ambient air temperature and humidity profiles and collected fog water at selected sites along a transect extending from the coast to the inland hyper-arid zone of the Desert, using automated sensors and fog collectors equipped with automated rain

gauges. Fog water does not penetrate very deeply so microorganisms may grow only in the top few mm of the soil. Within the extreme hyper-arid core (specifically the Lomas Bayas region) even fog water may be lacking for significant periods and soils collected recently from this area currently are being screened for bacteria. It has been shown previously that the reduction in available fog water along the coastal-inland transect is correlated with a reduced colonization rate for hypolithic cyanobacteria (Cáceres et al. 2007). The implications of geochemical and soil humification information reported in these presentations has obvious import for attempts to isolate and cultivate microorganisms from this hostile environment.

Microbiology

Two pioneers of Atacama Desert microbiology—Benito Gómez-Silva (University of Antofagasta) and Cecilia Demergasso (Universidad Católica del Norte, Antofagasta) considered how microorganisms have overcome the prevailing harsh conditions of the Desert to colonize a wide range of ecological niches. An important point made by Benito Gómez was the need to discriminate between extremophilic and extremotolerant microorganisms in the context of the microbial ecology of extreme environments, and his postulate that extremotolerants may have larger genetic and metabolic plasticity raises intriguing questions and will be answered as full genome sequences of these organisms become available. In terms of life-controlling factors in the Atacama Desert Gómez considers that liquid water and solar radiation are the major determinants while habitat availability, temperature and soil pH and toxicity have less significance (high localized concentrations of toxic elements such as arsenic as a result of natural occurrence or smelter waste being the exceptions). Tolerance to desiccation and intense irradiance are closely linked in the Atacama and avoidance strategies evolved by microorganisms include growth location (hypo- and endolithic), extracellular polymer synthesis, damage repair and pigmentation, the latter enabling epilithic colonization. Melanins are common to many actinobacteria genera isolated from salars and extreme hyper-arid sites while scytonemin has a comparable function in Atacama cyanobacteria. The ratio of scytonemin concentrations in epilithic to endolithic cyanobacteria

colonizing halite rock reaches 24:1 (Gómez-Silva 2010).

Cecilia Demergasso and her colleagues' recent investigations have focused on subsurface geomicrobiology and she reported results from the Ataca-Mars2009 Mars analogue drilling program at a site near the Salar de Grande. Cores up to 5 m deep were analyzed in situ using a biosensor chip comprised of an impressive bank of antibodies for detecting bacteria, archaea and a wide range of molecular biomarkers (Parro et al. 2011). The highest abundance of prokaryotes and biomarkers was detected at a depth of about 2 m in a hyper-saline habitat dominated by halite, nitrate and perchlorate salts. The significance of this particular geochemistry becomes apparent when its hygroscopic properties and hence deliquescence capacities are examined. Ingenious deliquescence assays made at low relative humidity showed that this capacity was greatest in the 2 m core sections and produced thin water films sufficient to support microbial growth. These experiments provide critical evidence to show that microorganisms in Atacama Desert environments can be present in metabolically active, proliferating states and not simply as dormant, non-functional populations. Corroboration of the biochip results was obtained by DAPI staining of core samples and 16S rDNA gene sequencing of environmental DNA. The most abundant clones comprised *Proteobacteria*, with smaller representation of *Firmicutes* and *Actinobacteria*. On the basis of these findings a model has been proposed for a hygroscopic, mineral-driven, hyper-saline, subsurface ecosystem fueled by reduced compounds of hydrothermal origin (hydrogen, hydrogen sulphide, acetate, formate) in which nitrates, sulphates and perchlorates could function as electron acceptors. This model has clear implications for the search for life in Martian soils. In addition Demergasso showed phylogenetic data obtained from sites the hyper-arid—arid margins of the Atacama Desert south-east of the Yungay; of considerable interest was the dominance (>70 %) of actinobacterial sequences in these soils.

Actinobacteria

The topic of actinobacteria was taken further in three presentations that also explored their biotechnological potential. Michael Goodfellow and colleagues

(Universities of Newcastle and Kent) have pioneered research on actinobacteria in the Atacama Desert (Okoro et al. 2009) and he emphasized the value of systematics for establishing their diversity in natural habitats and in designing improved procedures for selective isolation of key taxa. A major attraction of actinobacteria is their unrivalled capacity to synthesize natural products with a wide spectrum of bioactivities and it is argued that if diverse populations of actinobacteria are present in extreme habitats they are likely to produce new chemical entities. Sample pretreatment and selective media strategies have enabled the isolation of actinobacteria from salar and extreme hyper-arid soils and while population sizes are small (e.g. compared say to agricultural soils), taxonomic diversity is high. Currently members of at least 12 genera have been isolated, a high proportion of which represent apparently rare taxa and all of which contain new species. Species of *Streptomyces* are especially abundant in Atacama Desert habitats and the detection of a large, taxonomically distinct clade isolated from a region of the Salar de Atacama (Laguna de Chaxa) is exciting attention because the clade presents a widespread range of antibacterials of differing modes of action, and the probability that it is composed of salar-adapted ecovars. Novel natural products are starting to be detected in these Atacama actinobacteria (see below) while the predicted secondary metabolite biosynthetic capacity of the first, very recent whole genome sequence of one of the Salar de Atacama *Streptomyces* strains [Gilles van Wezel, Geneviève Girard, Leiden University (2012) personal communication] reinforces our optimism that these are organisms of choice for pharmacological screening campaigns. Catherine Lizama and Jorge González (Universidad de Antofagasta) are investigating actinobacterial diversity over a wide area of the Atacama Desert covering Regions I (Tarapacá) and II (Antofagasta). Despite using only a limited number of isolation media they recovered members of several genera of actinomycetes including *Nocardia*, *Microthricum*, *Prauserella* (notably not recorded by the UK group) and *Streptomyces*, over 50 % of which showed antibacterial activity; interesting in the latter context is the activity of some isolates against Gram negative bacteria. At another, northern part of the Salar de Atacama (Laguna Tebenquiche) that is hyper-saline and practically anoxic, they have isolated Archaea that have potential for carotenoid production. A natural

protection against radiation damage, these pigments have many biological functions that can be exploited in medicine, health foods, the food industry, and cosmetic formulations (Namitha and Negi, 2010). Martha Hengst and Cristina Dorador (Universidad de Antofagasta) described their search for new bioactive compounds produced by bacteria isolated from the northern altiplano of the Atacama Desert and pointed out the importance of dereplicating phenotypically ambiguous bacteria to facilitate efficient screening and to minimize costs and time in maintaining large culture collections. This strategy was illustrated with isolates of *Streptomyces* using the colour group differentiation procedure described previously by Goodfellow (Antony-Babu et al. 2012). One *Streptomyces* strain from the Salar de Tara (4,500 m) produced aminobenzoquinones (named abenquines) that contain rare combinations of benzoquinones and a range of amino acids. Antibacterial and antifungal activities of these compounds was weak but more interestingly abenquines showed inhibitory activity against type 4 phosphodiesterase (PDE4b) suggesting that they might be explored further in the context of inflammatory diseases (Schulz et al. 2011). The microbial mats of another high altitude salar, the Salar de Huasco (3,800 m) are dominated by members of the *Alphaproteobacteria*, specifically the *Roseobacter* clade. Hengst and Dorador postulate several roles for these bacteria in the salar community that may involve radiation protection, sulphur cycling, and regulation of the community structure by quorum sensing and the production of bioactive compounds. Preliminary screening of *Streptomyces* strains isolated from Salar de Huasco shows a high level of antibacterial, antifungal and cytotoxic activity, highlighting the potential of high-altitude lakes of the Atacama Desert as sources of new strains and bioactive substances.

Culture-independent studies

Success in culture-independent surveys of microorganisms in Atacama Desert habitats has been varied but analyses of this type are necessary for evaluating total population diversities and for predicting functional ecology. Analysis of five different wetlands located at high altitude across a latitudinal gradient using 16S rRNA clone libraries, revealed a high

microbial diversity dominated by *Proteobacteria* (Hengst and Dorador, unpublished data). Each of the wetlands studied exhibited a unique pattern of microbial diversity at phylotype level. Actinobacteria were present only in freshwater lakes. However, detailed analysis of a vertical section of a microbial mat from Salar de Huasco using 16S rRNA pyrosequencing (Dorador C, Vila I, Witzel K–P, Imhoff JF, unpublished results), revealed the presence of representatives of at least ten different actinobacteria genera (*Microcella*, *Arthrobacter*, *Cryobacterium*, *Frigobacterium*, *Dietzia*, *Nocardioides*, *Propionibacterium*, *Luteococcus*, *Kocuria* and *Patulibacterium*), where the higher abundance was detected at deeper, anoxic layers of the microbial mat. Existing methods used to isolate DNA typically underestimate the diversity of spore-forming bacteria including Actinomycetes. Therefore, it is likely that the diversity of actinobacteria in these systems is higher, especially considering the high variability and different microniches in the Atacama Desert wetlands.

The report of the AtacaMars 2009 project presented by Cecilia Demergasso provided a good example of the value of culture-independent analyses and more recently she has applied similar molecular methods to compare water and sediment samples from the Salar de Gorbea south east of Antofagasta. Although gammaproteobacteria dominated both communities, actinobacteria comprised a significant fraction of the sediment biota whilst being absent in the water community; this differential distribution of actinobacteria also is frequently found in deep-sea communities. The most recent example of this approach (Neilson et al. 2012) relates to the analysis of soils at the hyper-arid margin of the Desert east of Yungay with the objective of characterizing community structures using pyrosequencing methods and inferring their functional potential based on the observed phylogenetics. Once again a dominance of actinobacteria (>70 %) was reported and particularly interesting is the abundance of members of deep lineage actinobacteria at various sites, i.e. members of the families *Nutriliuraptoraceae*, *Conexibacteriaceae*, *Solirubrobacteraceae* and *Patulibacteraceae*, and the subclass *Rubrobacteridae*. Phylogenetic evidence obtained from one of the sites suggests the presence of chemoautotrophic taxa able to obtain energy via the oxidation of nitrite, carbon monoxide, iron and/or sulphur.

Habitat diversity

Given the size of the Atacama Desert (it extends from 15 to 30 °C and from sea level to ca. 3,500 m) it is not surprising that it contains a range of ecological niches several of which have their origins in and are characterized by volcanic geochemistry. Above this altitude the altiplano presents yet another diversity of ecological niches characterized by significantly higher relative humidity. Cecilia Demergasso and her colleagues have analyzed two such environments that contain arsenic and one of these, in the Salar de Ascotán, is an arsenic-rich evaporitic basin (ca. 3,700 m) in the High Andes of northern Chile. The group has obtained convincing microbiological and chemical evidence to challenge the orthodoxy that arsenic minerals such as orpiment (As₂S₃) have an abiotic origin (Demergasso et al. 2007). Thus, bacterial precipitation of arsenic sulfides is a geochemically relevant metabolism in this ecosystem but also may have biotechnological potential. For example, early trials with arsenic sulfide nanoparticles produced by *Fusibacter ascotence* have revealed selective effects on cancer cell lines (Serrano et al. 2012). Many questions concerning the ecological roles of microorganisms in the Atacama Desert remain to be answered. However, the increasing body of new data highlights the fact that these microorganisms are subject to extreme environmental fluctuations which likely drives changes in their population dynamics, function and diversity.

Novel chemical diversity

The natural product chemistry of Atacama Desert microorganisms is in its infancy and was discussed by Marcel Jaspars (Aberdeen University). He reiterated the view that organisms found in remote and extreme locations are potential sources new chemistry, a point illustrated impressively with reference to novel microbial metabolites recently isolated from deep-seas, volcanic springs, cryo-environments and a variety of industrial waste sites presenting hyper salinity, high pH and metal contamination. A bioassay guided isolation protocol based on partition fractionation of fermentation broths followed by size exclusion and HPLC can be used to detect and purify bioactive compounds, following which structure determination can be made using NMR and other spectroscopic

techniques. A complementary approach to biodiversity campaigns is to use chemistry to guide organism selection. In Jaspars' group MALDI-TOF mass spectrometry is employed for such biotyping and its potency demonstrated by the identification of a novel peptide produced by a member of a desert-signature actinobacterium—*Modestobacter*. However, to date most of the analyses have been made on members of the taxonomically distinct *Streptomyces* clade isolated from the Salar de Atacama (Rateb et al. 2011a, b). Bioactive ansamycins were discovered in *Streptomyces* sp. C34 on the basis of genome-mining experiments that targeted the gene encoding 3-amino-5-hydroxybenzoic acid (AHBA) synthase; these compounds, named chaxamycins after the Laguna de Chaxa sampling site, displayed promising antibacterial activities with chaxamycin D showing notable activity against clinical isolates of methicillin-resistant *Staphylococcus aureus*. The chaxamycins also inhibit the intrinsic ATPase activity of human heat shock protein Hsp90 thus revealing potential antitumor activity, corroborated by the results of virtual docking studies showing that chaxamycins docked into the ATP-binding pocket of Hsp90. The old tenet of 'what you find depends on how you look' is well exemplified by further research with *Streptomyces* sp. strain C34. The biosynthetic capacity of a single microorganism is maximized by varying fermentations conditions as a means of expressing otherwise silent genes, a strategy known as the one strain—many compounds approach. Applied to *Streptomyces* sp. C34 the approach has revealed a rare class of 22-membered macrolactone polyketides (chaxalactins) that are active against Gram positive bacteria. From another member of this *Streptomyces* clade a large molecular weight compound has been identified as a novel lasso peptide (N-terminal macrolactam rings through which are threaded C-terminal linear tails) (Jaspars, unpublished data). The 16-membered Atacama lasso peptide, like daptomycin and microcin J25, is antibacterial and its full bioactivity spectrum is currently under investigation.

Although very many microbial secondary metabolites express biological activity, the natural product per se frequently is not developed as a therapeutic drug. Reasons for this include insufficient potency and/or selectivity, toxicity, and poor pharmacokinetics that the intervention of medicinal chemistry may improve. The group of Juan Asenjo and Barbara Andrews (University of Chile, Santiago) has successfully developed systems

biology and metabolic engineering approaches (Moisset et al. 2012) to improve and modify the properties of natural products that now are being applied to actinobacteria from the Atacama Desert. Two of their co-workers Valeria Razmilic and Jean Franco Castro are carrying out projects in this area with the collaboration of several U.K. researchers including Alan Bull from Kent, Mervyn Bibb from Norwich, Marcel Jaspars from Aberdeen, Michael Goodfellow from Newcastle, and Gilles van Wezel and Geneviève Girard from Leiden. Valeria Razmilic is developing a genome scale model of the chaxamycin-producing *Streptomyces* sp. C34. Systems biology tools, such as flux balance analysis (FBA), will be used for in silico design to optimize fluxes (e.g. simulating gene knockouts) in particular to allow the metabolic shift from biomass or other primary or secondary metabolites to the production of the new polyketide analogues that will be produced through metabolic engineering and assessed for improved bioactivities. In a complementary project Jean Franco Castro is seeking to improve product formation of either chaxamycins or chaxalactins produced by *Streptomyces* sp. C34 by heterologous expression of the biosynthetic gene cluster of these antibiotics and by precursor engineering. The gene clusters involved in these syntheses will be characterized via bioinformatics tools and genome mining prior to making predicted gene knock-outs to enhance precursor production. On the basis of results with other bioactive-producing actinobacteria, heterologous expression of the redesigned biosynthetic gene cluster is anticipated to yield higher productivities of the target molecule.

A living not dead Desert

The hyper-arid regions of the Atacama Desert have from time to time been viewed, very mistakenly, as 'dead' and devoid of life; this notion can be dismissed emphatically as demonstrated by contributors to the Chile workshop. The inventory of microbial taxa isolated or detected in and upon Atacama soils, regoliths and rocks is expanding rapidly among which are represented most bacterial phyla (including cyanobacteria), Archaea, micro-fungi and lichens. However, their study remains beset by several challenges including effective isolation and cultivation, taxonomy and curation (regrettably a problem not restricted to Atacama organisms), and defining ecological function and

adaptation mechanisms. The latter issue is highly relevant in the Atacama context where organisms are challenged by multiple environmental extremes; such poly-extremotrophy (adaptation to more than two extremes) has received comparatively little attention by microbiologists. Continued research in this fascinating and beautiful environment undoubtedly will extend understanding of the microbial world and provide opportunities for developing new biotechnology.

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