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Extreme Environments

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Introduction

The study of extreme environments is an exploration of the limits of life. Organisms perform a number of basic functions (homeostasis, metabolism, growth, reproduction, etc.), and our water- and carbon-based systems are constrained within certain environmental parameters. Some organisms can push the limits of these environmental boundaries and thrive in what to most other living things are conditions inimical to life. Thus the concept of "extreme" environment is necessarily relative to conditions under which most species thrive. Organisms that live in relatively hostile environments (called extremophiles) include archaea and bacteria, but other groups of organisms also have members that can live in relatively stressful habitats. Scientists point out that there is a difference between living under extreme conditions and tolerating (perhaps by going dormant) extreme conditions, but both situations can help us understand how extreme environments affect life. The adaptations that allow organisms to live in (or survive) extreme conditions are targets of scientific study because they help us understand life's basic processes and how life responds to environmental challenges. The lessons we learn have important applied aspects because they can help us grow food, process wastes, restore disturbed habitats, and perform many other vital tasks. In this article, we provide sections based on particularly important stress factors, but we also have included sections in which the focus is on major concepts, to show how organisms from extreme environments can inform other areas of scientific interest.

General Overviews

Each of life's many parameters may reach extreme conditions, so that there are many resources focused on single factors or particular extreme habitats. Certainly, astrobiology considers the environmental limits of life at great extremes and thus is a rich source of information on how life responds to environmental challenges: Catling 2013 is a relatively brief overview of the broad field of astrobiology. Some single-factor overviews are included in our coverage of factors in this article (see subheadings under Major Stressors). Many overviews are based on habitats and are one way to explore particular stresses characteristic of certain habitats. Bell 2012 contains an excellent collection of chapters, each focusing on a particular extreme habitat. Additional examples of habitat-based resources include coverage of deep-sea hydrothermal vents in Van Dover 2000 and deserts in Ward 2009. Rajakaruna, et al. 2014 discusses extremophiles in the context of stressful soils derived from rocks with unusual chemistries (see also the *Oxford Bibliographies* in Ecology article "Geoecology," especially the section on extremophiles). Other overviews focus on adaptations of major groups of organisms to extreme environments. As examples, Rajakaruna, et al. 2014 provides good coverage for plants (and some associated groups, such as lichens and mycorrhizae), whereas Riesch, et al. 2015 covers teleost fishes. Bakermans 2015 is a general introduction to extremophile microbes, covering all types of extremophiles, while Rampelotto 2012–2014 provides a number of review papers regarding microbes, but also some on eukaryotic organisms and their adaptations to extreme conditions. There is a strong conceptual connection between extreme environments and their effects on organisms in creating environmental stress: Schulte 2014 provides an overview of the difficulty of defining environmental stress, as well as its importance for understanding how organisms adapt to environmental extremes.

Bakermans, Corien, ed. 2015. *Microbial evolution under extreme conditions*. Life in Extreme Environments 2. Berlin: De Gruyter.

The thirteen chapters in this edited book provide an excellent introduction to microbes in extreme environments. Chapters deal with extreme temperature, pH, salinity, and radiation, as well as multiple extremes and evolutionary mechanisms.

Bell, Elanor M., ed. 2012. *Life at extremes: Environments, organisms, and strategies for survival*. CABI Invasive Species 1. Wallingford, UK: CABI.

This edited book contains twenty-eight chapters, most of which focus on a single extreme habitat. Thus, valuable introductions are provided to the stressors in each habitat and to the adaptations of organisms living in them that allow these organisms to withstand extreme environments.

Catling, David C. 2013. *Astrobiology: A very short introduction*. Very Short Introductions 370. New York: Oxford Univ. Press.

Part of a series of concise overviews, this book provides brief coverage of the major topics in astrobiology and is a good entry point into the contributions of astrobiology to our understanding of life in extreme environments.

Rajakaruna, Nishanta, Robert S. Boyd, and Tanner B. Harris, eds. 2014. *Plant ecology and evolution in harsh environments*. Environmental Research Advances. Hauppauge, NY: Nova Science.

This book synthesizes current scientific knowledge about a broad spectrum of harsh environments for plants (along with lichens and mycorrhizae). It includes chapters on techniques as well as particular types of stresses and thus is a good entry point into the literature for plants in extreme environments.

Rampelotto, Pabulo H., ed. 2012–2014. *Special issue: Extremophiles and extreme environments*. *Life*.

This "special issue," which in fact is spread out over six issues of the journal, contains twenty-four papers that together provide a good overview of extreme environments and the organisms in them. Fifteen of the papers appear in *Life* 3.1 (2013), with another three both in 3.2 and 3.3 (2013) and single articles in 2.3 and 2.4 (2012) and 4.1 (2014). Most of the papers deal with microbes, but the mix of reviews along with a few research articles provides entry to many pertinent subjects.

Riesch, Rüdiger, Michael Tobler, and Martin Plath, eds. 2015. *Extremophile fishes: Ecology, evolution, and physiology of teleosts in extreme environments*. New York: Springer.

This book explores how fishes survive harsh environmental conditions, including a wide variety of unusual stressful habitats. It also explores specific adaptations as well as the role of harsh environments in speciation and the connection between extreme environments and conservation.

Schulte, Patricia M. 2014. What is environmental stress? Insights from fish living in a variable environment. In *Special issue: Stress: Challenging homeostasis*. *Journal of Experimental Biology* 217.1: 23–34.

Using Atlantic killifish as a model organism, the author reviews biological definitions of environmental stress. She also demonstrates how study of this fish has revealed the roles of adaptation and phenotypic plasticity in allowing it to thrive in a habitat that is hypervariable in temperature, salinity, and oxygenation.

Van Dover, Cindy Lee. 2000. *The ecology of deep-sea hydrothermal vents*. Princeton, NJ: Princeton Univ. Press.

A broad overview of the history and biology of these fascinating and famous extreme environments, this book is a good introduction to these habitats and the organisms in them. The author also discusses ecology and community dynamics in these unique habitats.

Ward, David. 2009. *The biology of deserts*. Biology of Habitats. Oxford: Oxford Univ. Press.

An example from a useful series of books, each focusing on a particular type of habitat, this one is an introduction to deserts and the organisms that inhabit them. It provides an entryway into the adaptations of desert organisms to the thermal and moisture stresses that characterize this habitat.

Journals

Papers regarding extreme environments can be found in a wide range of journals, many of which contain papers on extremophile microbes. For example, the widely cited microbiological journal *Journal of Bacteriology* periodically publishes research on bacteria that inhabit extreme environments. But in particular, *Extremophiles* is an excellent source that is devoted to that specific topic. *Astrobiology* contains information regarding extremophile microbes but also includes papers on the broader topics of what environmental factors (and other factors) limit life in the universe, and even how we might transform currently lifeless planets into Earthlike planets (the process of terraforming). Other journals focus on particular types of stress: *Journal of Thermal Biology* is an example that includes papers on how humans and other animals deal with thermal stress and its physiological, ecological, and evolutionary consequences (among other relevant topics). Still other journals emphasize particular areas of stress biology: for example, the *Journal of Stress Physiology & Biochemistry* examines physiological and biochemical stress responses both of plants and animals, while *Cell Stress and Chaperones* in a good source for articles focusing on cellular-level effects of stress on a broad array of organisms. As another example, the journal *Physiology* includes review articles that target physiological adaptations to environmental extremes. Papers regarding the evolution of tolerance to extreme environments can sometimes be found in *Evolution*, a journal that covers adaptation to many biotic and abiotic factors and also includes theoretical articles and reviews.

***Astrobiology*.**

Covers research on a broad array of topics, including the origin, evolution, distribution, and potential future of life in the universe.

***Cell Stress and Chaperones*.**

Covering stress at the cellular level, this journal is a good source of papers covering a wide range of animal, microbe, and plant species and including both basic and applied research.

***Evolution*.**

A journal broadly covering evolution, published on behalf of the Society for the Study of Evolution, it contains research and review articles that occasionally target adaptations to extreme environmental conditions.

***Extremophiles*.**

Focusing on microbiology, this journal’s papers cover a variety of extreme conditions. Topics include molecular biology, structure, function, community composition, and applications of extremophiles for environmental remediation and other human uses.

***Journal of Bacteriology*.**

One of a suite of microbiological journals published by the American Society for Microbiology (many of which publish papers pertinent to microbes in extreme environments), this journal regularly publishes papers on extremophile bacteria as well as more-general topics such as mechanisms of bacterial stress tolerance.

***Journal of Stress Physiology & Biochemistry*.**

This journal covers physiological and biochemical stress responses of plants and animals, publishing methods and experimental articles.

***Journal of Thermal Biology*.**

Focusing on temperature as an environmental factor, this journal includes papers relevant to thermal stress and its effects on many aspects of biology.

***Physiology*.**

Published by the American Physiological Society, this journal contains invited reviews that provide excellent summaries in the broad field of physiology. Some reviews target physiological responses to extreme environments and are useful overviews of the literature.

Major Stressors

The study of abiotic stress tolerance has received much attention because the understanding of how organisms survive and even thrive under extremes can provide valuable insights into evolution, conservation, and biotechnological applications (see subsections under Broad Themes). The concept of an “extreme” environment is relative and thus difficult to precisely define: Rampelotto 2013 defines extreme conditions as those under which the vast majority of other organisms would not be able to survive. Thus, extremes can be described for many of the parameters affecting life, such as Temperature, pH, High Pressure, ionizing Radiation, Salinity, Water Availability, Oxygen availability, and toxic Heavy Metals. Exact thresholds are sometimes provided for some factors by some authors, but it is best to consider life as occurring across a continuum of environmental conditions. Thus, what constitutes an extreme is necessarily relative, and thresholds are not particularly useful. Furthermore, there may be relatively sharp gradients in environmental factors, and this provides niches that are intermediate in nature. As an example for microbes, Brune, et al. 2000 discusses oxic-anoxic interfaces and how they can affect microbial populations and provide special microniches. In this section, the subheadings isolate individual abiotic environmental factors, and we provide an overview for each that is designed to aid in accessing the extensive information available. Almost all the factors listed may affect life if levels are too high or too low (with the exception of ionizing radiation), but for some (pressure, salinity, heavy metals), most attention has dealt with stress produced by high levels of these factors, and so that is what we emphasize in our coverage. We also point out that much of the coverage of extremophiles has focused on microbes: Horikoshi, et al. 2011 and Rampelotto 2013 provide excellent overviews on the diversity and the ecology of extremophiles and how they are able to deal with extremes in major abiotic stressors. These microbes may play major roles in environmental problems: for example, Baker and Banfield 2003 discusses the role of microbes in acid mine drainage. Despite the early emphasis on microbes, more attention is now being paid to nonmicrobial life, and we have included information on as many other types of organisms as was practicable. Finally, some extremophiles are able to withstand extremes in more than one of the environmental conditions. These polyextremophiles have adaptations that help them resist multiple stresses, which are covered in a separate section (Polyextremophiles).

Baker, Brett J., and Jillian F. Banfield. 2003. Microbial communities in acid mine drainage. *FEMS Microbiology Ecology* 44.2: 139–152.

The review focuses on the diversity, ecology, physiology, genetics, and evolution of autotrophic and heterotrophic archaea and bacteria that thrive in metal-rich, acid mine drainage–contaminated habitats.

Brune, Andreas, Peter Frenzel, and Heribert Cypionka. 2000. Life at the oxic–anoxic interface: Microbial activities and adaptations. *FEMS Microbiology Reviews* 24.5: 691–710.

This review examines how gradients in a vital environmental feature (oxygen availability) affect microbial communities and have important ramifications for biogeochemical cycling. The authors focus on three case studies (sediments, aquatic plant rhizospheres, and the intestinal tracts of insects) to illustrate these features.

Horikoshi, Koki, Garabed Antranikian, Alan T. Bull, Frank T. Robb, and Karl O. Stetter, eds. 2011. *Extremophiles handbook*. Springer Reference. Tokyo: Springer.

An excellent general introduction to extremophiles, the book provides broad coverage of the taxonomy, ecology, physiology, biochemistry, and genetics both of microbial and eukaryotic species tolerant of extremes in temperature, pH, salinity, pressure, and other major stressors.

Rampelotto, Pabulo Henrique. 2013. Extremophiles and extreme environments. In *Special issue: Extremophiles and extreme environments*. *Life* 3.3: 482–485.

This editorial is a good overview of extreme environments and highlights the organisms in each domain of life that survive in such habitats. It also discusses novel techniques in molecular biology that have enabled advances in the study of extremophiles.

Temperature

Extreme temperatures create many challenges for the survival, growth, and fecundity of organisms. From degradation of chlorophyll and denaturation of proteins and nucleic acids at high temperatures, to structural deformation caused by ice crystal formation at freezing temperatures, organisms may either adapt or perish in these extremes. Rampelotto 2013 (cited under Major Stressors) points out that thermal preferences vary greatly and encompass thermophiles (organisms that reach maximum growth between 60–80°C, such as the blue-green alga *Synechococcus lividis*), hyperthermophiles (e.g., the archaea *Pyrolobus furnarii*, whose maximum growth is reached at 113°C), and psychrophiles (organisms such as *Psychrobacter* and some insects, for which maximum growth occurs below 15°C). Organisms in all domains of life—bacteria, archaea, and eukarya—can face environmental stresses such as thermal extremes. Microbes in particular have received extensive attention, and Reysenbach, et al. 2013 is an excellent general introduction to our knowledge of thermophilic microorganisms, while Margesin and Miteva 2011 provides a review of psychrophilic microbes. Zilberstein and Shapira 1994 highlights the effects of temperature on parasites, while Bale 2002 explores the effects of low temperatures on insects and advances since the late 20th century in the physiological, biochemical, and ecological dimensions of insect cold hardiness. Habitats such as deep-sea environments, deserts, and high-altitude glaciers create perpetual extreme temperature environments. Campbell, et al. 2009 suggests submarine hydrothermal vents as model systems for studying microbial communities and the adaptations that enable life in an extreme environment that is akin to archaean conditions. Körner and Larcher 1988 provides an overview of the structural characteristics and functional attributes of plants in cold environments. For an overview of thermoresistance in the model organism *Drosophila*, see Hoffmann, et al. 2003, an examination of adaptation to thermal extremes across populations and species in that genus. The adaptations of thermophiles to extreme temperatures are a result of many different strategies, and early-21st-century advances in genomic studies have enabled a more holistic understanding of these mechanisms. Wang, et al. 2015 summarizes survival mechanisms of thermophiles from an omics perspective, which combines genomic, proteomic, and transcriptomic analyses into a multidimensional cooperative model.

Bale, Jeffrey S. 2002. Insects and low temperatures: From molecular biology to distributions and abundance. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 357.1423: 849–862.

This paper provides an overview of the physiological and biochemical mechanisms governing insect cold hardiness, as well as descriptions of discoveries since the late 20th century in the effects of temperature on insects, and suggests applications of this ecological knowledge in light of climate warming.

Campbell, Barbara J., Julie L. Smith, Thomas E. Hanson, et al. 2009. Adaptations to submarine hydrothermal environments

exemplified by the genome of *Nautilia profundicola*. *PLoS Genetics* 5.2: e1000362.

The authors employ phylogenetic techniques to analyze the genome of a hyperthermophilic chemoautotroph found in deep-sea hydrothermal vents, and they categorize the genomic properties that enable life at an extreme temperature 2,500 meters under the ocean.

Hoffmann, Ary A., Jesper G. Sørensen, and Volker Loeschcke. 2003. Adaptation of *Drosophila* to temperature extremes: Bringing together quantitative and molecular approaches. *Journal of Thermal Biology* 28.3: 175–216.

In this novel study that combines laboratory studies and studies under natural conditions, the authors examine previous research of *Drosophila* adaptation to thermal extremes and develop linkages between the genetic and physiological basis for interspecific and intraspecific evolutionary response to thermoresistance.

Körner, Christian, and Walter Larcher. 1988. Plant life in cold climates. *Symposia of the Society for Experimental Biology* 42:25–57.

This fundamental paper outlines the structural and functional properties of plants in low-temperature conditions that enable their adaptation and survival in extreme environments such as high mountains and tundra regions.

Margesin, Rosa, and Vanya Miteva. 2011. Diversity and ecology of psychrophilic microorganisms. *Research in Microbiology* 162.3: 346–361.

An excellent overview of microbes adapted to low-temperature environments, this review surveys psychrophiles by habitats occupied and also provides information on ecology, biogeography, and the mechanisms that adapt microbes to cold habitats.

Reysenbach, Anna-Louise, Mary Voytek, and Rocco Mancinelli, eds. 2013. *Thermophiles: Biodiversity, ecology, and evolution*. New York: Springer.

Originally published in 2001, this edited volume is a useful introduction to a wide range of topics regarding thermophilic microorganisms. Its fourteen chapters provide easy entry to the literature focusing on the hyperthermophiles, which have been so valuable both for theoretical and applied scientific advances.

Wang, Quanhui, Zhen Cen, and Jingjing Zhao. 2015. The survival mechanisms of thermophiles at high temperatures: An angle of omics. *Physiology* 30.2: 97–106.

This excellent review summarizes the physiological mechanisms used by thermophiles, organisms that achieve optimum growth above 60°C, and suggests that a cooperative model consisting of multidimensional regulations encompasses their adaptability to extreme temperature.

Zilberstein, Dan, and Michal Shapira. 1994. The role of pH and temperature in the development of *Leishmania* parasites. *Annual Review of Microbiology* 48:449–470.

In this review, the authors investigate the effect of extreme pH and temperature on the protozoan parasite *Leishmania* and highlight the morphological, molecular, and developmental alterations caused by temperature-induced gene expressions.

pH

Most organisms live in a narrow range of pH near neutrality (pH = 7.0); acute or chronic exposure to acidity (pH less than 7.0) or alkalinity (pH greater than 7.0) can adversely affect physiological functions. The pH is important for determining the solubility and bioavailability of chemical constituents such as essential nutrients and toxic heavy metals. Extremes in pH can therefore cause physiological stress to organisms due to ion deficiencies or toxicities influencing membrane function and cellular metabolic processes. Organisms able to handle extremes in acidity (acidophiles; pH less than 3.0) or alkalinity (alkaliphiles; pH greater than 9) possess fundamentally different molecular structures and physiological controls for pH homeostasis in comparison to close relatives found in habitats with near-neutral pH. Padan, et al. 2005 is an excellent review of alkali tolerance in bacteria, highlighting the approaches, major findings, and unresolved questions in alkaline pH homeostasis. Similarly, Cotter and Hill 2003 describes the mechanisms involved in tolerating high acidity among gram-positive bacteria, emphasizing how an understanding of acid resistance mechanisms can aid in engineering strains able to thrive or perish under low pH conditions. Acidification of freshwater systems is a global threat to aquatic biodiversity, and Kwong, et al. 2014 examines the adaptive mechanisms promoting extreme acid tolerance in fish, including the molecular basis of ionic and acid-base regulation. Alternatively, Wilkie and Wood 1996 covers aspects of alkalinity tolerance in fish, including adjustments to nitrogenous waste metabolism and excretion as well as modifications to gill function and morphology. Pierce 1993 examines the effects of acidity on amphibian communities, showing that pH effects vary developmentally depending on complex interactions with other physical, chemical, and biological factors. Acidic soils are a leading cause for poor plant growth and lower crop yields in many parts of the world. Bian, et al. 2013 reviews toxic effects of acidity on plants, including early-21st-century research on mechanisms of plant tolerance to acidity and associated aluminum toxicity. Bignell 2012 is a good overview of pH tolerance in fungi, focusing on the most-recent advances in physiology and genetics of pH adaptation. Gross 2000 covers how acid-tolerant and acidophilic algae deal with high-acid environments, including the mechanisms employed to deal with low carbon dioxide, high heavy metals, and low nutrients often associated with acidic habitats.

Bian, Miao, Meixue Zhou, Dongfa Sun, and Chengdao Li. 2013. Molecular approaches unravel the mechanism of acid soil tolerance in plants. *Crop Journal* 1.2: 91–104.

The review is an excellent source for then-recent findings on acid and aluminum tolerance in plants, including external and internal mechanisms and their underlying genetic bases. Early-21st-century advances in marker development and the impacts of marker-assisted selection in breeding acid-tolerant crops are also discussed.

Bignell, Elaine. 2012. The molecular basis of pH sensing, signaling, and homeostasis in fungi. *Advances in Applied Microbiology* 79:1–18.

The review shows how fungal pH tolerance is mediated by distinct but complementary homeostatic responses and highly conserved intracellular signaling pathways. Early-21st-century advances in molecular understanding of pH sensing, signaling, and homeostasis are also highlighted.

Cotter, Paul D., and Colin Hill. 2003. Surviving the acid test: Responses of gram-positive bacteria to low pH. *Microbiology and Molecular Biology Reviews* 67.3: 429–453.

This review highlights how gram-positive bacteria counter the negative impacts of low cytoplasmic pH, including loss of ability to produce adenosine triphosphate (ATP) and structural damage to cell membranes and macromolecules. How this knowledge can be used to aid or prevent bacterial survival in acid environments is also discussed.

Gross, Wolfgang. 2000. Ecophysiology of algae living in highly acidic environments. *Hydrobiologia* 433 (August): 31–37.

A review focusing on how acidophilic algae deal with the limited supply of carbon dioxide, high concentrations of heavy metals, and low nutrient availability characteristic of high-acidity environments.

Kwong, Raymond W. M., Yusuke Kumai, and Steve F. Perry. 2014. The physiology of fish at low pH: The zebrafish as a model

system. In *Special issue: Stress: Challenging homeostasis*. *Journal of Experimental Biology* 217.1: 651–662.

A review examining the effects of acidity on freshwater fish and the adaptive mechanisms promoting extreme acid tolerance in fishes native to acidic environments. Mechanisms regulating ionic and acid-base balance during acid exposure are investigated, using zebrafish as a model system.

Padan, Etana, Eitan Bibi, Masahiro Ito, and Terry A. Krulwich. 2005. Alkaline pH homeostasis in bacteria: New insights. *Biochimica et Biophysica Acta: Biomembranes* 1717.2: 67–88.

This review on bacterial adaptations to extreme alkaline settings focuses on what transcriptome and proteome analyses, alongside physiological and genetic studies, have revealed about alkaline pH homeostasis in a number of well-characterized alkali-tolerant and extremely alkaliphilic bacteria.

Pierce, Benjamin A. 1993. The effects of acid precipitation on amphibians. *Ecotoxicology* 2.1: 65–77.

This older review on acid tolerance in amphibians shows there is interspecific and intraspecific variation in acid sensitivity and that effects vary developmentally and depend on complex interactions with other environmental factors. The importance of investigating the potential role of sublethal effects of acidity on amphibian declines is also highlighted.

Wilkie, Michael P., and Chris M. Wood. 1996. The adaptations of fish to extremely alkaline environments. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* 113.4: 665–673.

A useful review that summarizes known mechanisms of alkalinity tolerance in fish, including adjustments to nitrogenous waste metabolism and excretion patterns as well as modifications to gill functional morphology.

High Pressure

Hydrostatic pressure varies from 1 atmosphere (atm) at the surface of the Earth to 1,100 atm at the bottom of the deep sea, with an average pressure in the ocean of 380 atm. While high-pressure environments compose the majority of the biosphere, interest in survival strategies and adaptations of organisms in high-pressure environments has surged only since the late 20th century. This acceleration is due to technological advances allowing human access to these habitats and to increased biotechnological applications of organisms adapted to high pressure (see Applied Uses of Extremophiles). Somero 1992 provides an excellent overview of shallow- and deep-sea species' resistance to high hydrostatic pressure (HHP) and examines the implications for distribution limits and biological organization in these habitats. Pradillon 2012 summarizes the mechanisms and survival strategies necessary for organisms living in high-pressure environments. Organisms that thrive in HHP habitats are called piezophiles or barophiles, and their response to high pressure can be either innate or acquired. HHP habitats include the depths of the ocean, such as in ocean trenches, as well as underground habitats and deep lakes. The Mariana Trench hosts organisms that can tolerate immense pressure (and low temperature) at 11,000 meters below the ocean surface. Kato, et al. 1998 provides the first evidence of the existence of *Moritella*, an obligately extreme-barophile bacterium found in the Mariana Trench. The hadal zone extends from 6,000 to almost 11,000 m beneath the ocean surface and harbors an array of fauna, including prokaryotics and amphipods. Blankenship-Williams and Levin 2009 summarizes hadal trench ecology from sixty years of sporadic sampling. Early-21st-century advances in deep-sea exploration and genomic techniques have enabled novel studies of microbial adaptations to HHP. Picard and Daniel 2013 summarizes the literature on microbial survival across geological time scales, highlighting both dynamic and static pressures from early to modern Earth. Simonato, et al. 2006 reviews then-recent findings in understanding microorganism adaptations to high-pressure environments from a genomic perspective. Oger and Jebbar 2010 focuses on microorganisms adapted to extreme pressure conditions in oceanic waters under a pressure of 100 atm or greater, and provides a synthesis of their many adaptations to HHP. Significant interest in responses to HHP has emerged in biotechnology. Mota, et al. 2013 highlights the applications of adaptations to HHP, such as altering microbial metabolic pathways to withstand high hydrostatic pressure, with important implications for biotechnological and industrial purposes.

Blankenship-Williams, Lesley E., and Lisa A. Levin. 2009. Living deep: A synopsis of hadal trench ecology. *Marine Technology Society Journal* 43.5: 137–143.

This paper covers biogeographical trends in the hadal zone—6,000 to almost 11,000 m below the ocean surface—from the previous sixty years and explores the faunal ecology of these deep-sea trenches.

Kato, Chiaki, Lina Li, Yuichi Nogi, Yuka Nakamura, Jin Tamaoka, and Koki Horikoshi. 1998. Extremely barophilic bacteria isolated from the Mariana Trench, Challenger Deep, at a depth of 11,000 meters. *Applied and Environmental Microbiology* 64.4: 1510–1513.

This exciting study uses two strains of extremely barophilic bacteria collected 11,000 m below the ocean surface. Multiple phylogenetic and experimental methods were employed to analyze adaptations, and the first evidence of the genus *Moritella* from these depths was reported.

Mota, Maria J., Rita P. Lopes, Ivonne Delgadillo, and Jorge A. Saraiva. 2013. Microorganisms under high pressure—adaptation, growth and biotechnological potential. *Biotechnology Advances* 31.8: 1426–1434.

In this comprehensive review, the authors report influential findings from the previous three decades of microorganisms' ability to grow and withstand high-pressure conditions, in the context of applied biotechnological uses. They highlight potential applications such as the development of novel compounds that respond to extreme pressure conditions.

Oger, Philippe M., and Mohamed Jebbar. 2010. The many ways of coping with pressure. *Research in Microbiology* 161.10: 799–809.

This excellent review compiles the strategies and adaptations of microorganisms for coping with HHP. Using carefully selected examples, it covers current knowledge of the mechanics and physiology of piezophiles and calls for further research to fill gaps in our understanding of adaptation to HHP.

Picard, Aude, and Isabelle Daniel. 2013. Pressure as an environmental parameter for microbial life—a review. In *Special issue: Biomolecular systems under extreme environmental conditions*. *Biophysical Chemistry* 183 (15 December): 30–41.

In this paper, the authors summarize hydrostatic-pressure conditions faced by microbes life since their infancy to the early 21st century and discuss their survival throughout time under dynamic pressure changes. The biogeochemical impact of microbes is also discussed in relation to changes in the deep ocean's hydrostatic pressure.

Pradillon, Florence. 2012. High hydrostatic pressure environments. In *Life at extremes: Environments, organisms, and strategies for survival*. Edited by Elanor M. Bell, 271–295. CABI Invasive Species 1. Wallingford, UK: CABI.

This chapter covers a broad range of mechanisms necessary for survival at HHP and explains the implications of these adaptations for life history strategies and evolutionary consequences.

Simonato, Francesca, Stefano Campanaro, Federico M. Lauro, et al. 2006. Piezophilic adaptation: A genomic point of view. In *Special issue: Aspects of prokaryotic genome research: 2nd European Conference on Prokaryotic Genomes*. *Journal of Biotechnology* 126.1: 11–25.

This well-rounded review uses multiple genomic approaches to summarize then-recent findings in microbial adaptations to high-pressure environments, asserting that while such advances in genomics provide many answers, they also produce many more questions.

Somero, George N. 1992. Adaptations to high hydrostatic pressure. *Annual Review of Physiology* 54:557–577.

In this highly influential paper, threshold pressures and physiological responses are investigated and found to differ greatly between shallow- and deep-living species. The interspecific differences in adaptations to high pressures become apparent at depths of 500 m, and these have implications for biological organization and distribution in aquatic habitats.

Radiation

Ionizing radiation (IR) consists of particles or photons that have adequate energy to interact with atoms and to remove electrons, thus producing ions and often disrupting bonding in molecules. Biological effects differ depending on the nature of the radiation and its dose but often result in disruption of metabolic processes: especially harmful is damage to DNA. But organisms have antioxidant molecules and DNA-repair mechanisms that can counter these harmful effects, with some organisms possessing extraordinary abilities to withstand the effects of IR (and thus being relatively radioresistant). As an overview, Kiefer 1990 reviews the physics of radiation and provides broad coverage of its effects on cells and whole organisms (emphasizing humans). Reisz, et al. 2014 provides a review of the effects of IR on biomolecules and includes useful information on how we detect those impacts, as well as showing how this information is critical to IR therapies in medicine. Prokaryotes are the most radiation-resistant organisms known; as a result, much research on the mechanisms of radioresistance has used bacteria and archaea. Confalonieri and Sommer 2011 provides a broad overview of the prokaryotes found to be radioresistant and the mechanisms involved in that resistance, while Byrne, et al. 2014 is an in-depth review of genes involved in conferring radioresistance to the model bacterium *Escherichia coli*. Dadachova and Casadevall 2008 reviews IR resistance in fungi, showing that some fungi even display directional growth in response to IR. The development of nuclear weapons and nuclear energy and the use of radiation for human health purposes have increased exposure of organisms to IR. Accidental releases of radioactivity, such as at Chernobyl in 1986, have provided opportunities to learn about effects of IR on organisms. For example, Zaitsev, et al. 2014 examines data on soil communities from sites experiencing radioactive pollution, proposing a system of biomonitors that can be used for determining environmental consequences of pollution events. In combination with genetic-engineering techniques, our knowledge of bacterial genes conferring resistance is allowing us to modify tolerance of non-extremophiles to allow them to better withstand environmental stress. For example, Pan, et al. 2009 uses a gene from the radioresistant extremophile *Deinococcus radiodurans* to produce salt-tolerant strains of the model bacterium *Escherichia coli* (more commonly known as *E. coli*), as well as the crop plant *Brassica napus* (rapeseed). Other radioresistant organisms may be useful in cleaning sites contaminated with radionuclides: Rivasseau, et al. 2013 shows that a newly described hyperradioresistant green alga can be used to accumulate radionuclides and purify nuclear effluents.

Byrne, Rose T., Stefanie H. Chen, Elizabeth A. Wood, Eric L. Cabot, and Michael M. Cox. 2014. *Escherichia coli* genes and pathways involved in surviving extreme exposure to ionizing radiation. *Journal of Bacteriology* 196.20: 3534–3545.

Using a model bacterial system, the authors identify many genes that confer tolerance to radiation. They conclude that radioresistance stems from multiple factors, and in this case they identify genes involved in a suite of cellular structures and functions.

Confalonieri, Fabrice, and Suzanne Sommer. 2011. Bacterial and archaeal resistance to ionizing radiation. *Journal of Physics: Conference Series* 261:012005.

A useful review of how radiation damages cells and how cells can tolerate or repair that damage. The authors also analyze the evolution of radioresistance, discuss mechanisms by which resistance occurs, and compare radioresistance between major groups of prokaryotes.

Dadachova, Ekaterina, and Arturo Casadevall. 2008. Ionizing radiation: How fungi cope, adapt, and exploit with the help of melanin. In *Special issue: Growth and development: Eukaryotes/prokaryotes*. *Current Opinion in Microbiology* 11.6: 525–531.

An excellent review of the effects of ionizing radiation on fungi, in which the authors explore fungal radioresistance, its intriguing association with the pigment melanin, the occurrence of fungi on spacecraft, and the fascinating phenomenon of radiotropism in fungi associated with the Chernobyl radiation disaster.

Kiefer, Jürgen. 1990. *Biological radiation effects*. Berlin: Springer-Verlag.

Although somewhat dated, this book provides a good introduction to the physics and chemistry of radiation, as well as an overview of its biological effects. Reflecting the importance of radiation as a pollutant and a medical tool, human effects are emphasized.

Pan, Jie, Jin Wang, Zhengfu Zhou, et al. 2009. IrrE, a global regulator of extreme radiation resistance in *Deinococcus radiodurans*, enhances salt tolerance in *Escherichia coli* and *Brassica napus*. *PLoS ONE* 4.2: e4422.

Illustrating the usefulness of radiotolerance genes in genetic engineering, the authors insert the IrrE gene into the model bacterium *E. coli* and the crop plant *Brassica napus*. They find that the modified organisms are much more salt tolerant, and they also explore the mechanisms of this tolerance.

Reisz, Julie A., Nidhi Bansal, Jiang Qian, Weiling Zhao, and Cristina M. Furdui. 2014. Effects of ionizing radiation on biological molecules—mechanisms of damage and emerging methods of detection. *Antioxidants & Redox Signaling* 21.2: 260–292.

In this review regarding how radiation affects biomolecules, the authors explore how “omics” technologies have revolutionized our understanding of these effects and our ability to detect and study them. These advances are particularly important for applied use in human medicine.

Rivasseau, Corinne, Emmanuel Farhi, Ariane Atteia, et al. 2013. An extremely radioresistant green eukaryote for radionuclide bio-decontamination in the nuclear industry. *Energy & Environmental Science* 6.4: 1230–1239.

The extremophile *Coccomyxa actinabiotis*, isolated from a nuclear facility, withstands as much ionizing radiation as the prokaryote *Deinococcus radiodurans*. Furthermore, it strongly accumulates radionuclides, and the authors show its usefulness for biodecontamination of nuclear wastes.

Zaitsev, Andrei S., Konstantin B. Gongalsky, Taizo Nakamori, and Nobuhiro Kaneko. 2014. Ionizing radiation effects on soil biota: Application of lessons learned from Chernobyl accident for radioecological monitoring. *Pedobiologia* 57.1: 5–14.

This review summarizes findings from studies of nuclear-accident locations to provide information on the sensitivity of various groups of soil organisms to levels and types of radioactive pollution. The authors propose a soil-biomonitoring system that can help us evaluate the environmental consequences of radioactive-pollution events.

Salinity

Saline environments pose two major difficulties for biological function: first, high salinity causes osmotic challenges, decreasing an organism’s ability to take up water; second, high concentrations of sodium (Na^+) and chloride (Cl^-) can impose specific ion effects, impairing metabolic processes and decreasing physiological efficiency. Various morphological, physiological, and biochemical adaptations enable halophilic organisms to survive and complete their life cycles in saline environments. There is significant research on halophytes, plants tolerant of salt concentrations over 200 millimolar NaCl. Although most of the water on Earth is saline due to exposure to seawater or secondary salinization due to unhealthful agricultural practices, only about 0.2 percent of all plant species are halophytic. Although such species are a rare phenomenon, Saslis-Lagoudakis, et al. 2014 (cited under Evolutionary Aspects of Extremophiles) shows that salt tolerance is found in a broad range of plant families, with relatively numerous instances of independent evolutionary origins and losses. Flowers and Colmer 2015 is an excellent overview of molecular, biochemical, and physiological mechanisms contributing to salt tolerance. Globally, salinity is a major challenge to agricultural productivity; Munns and Gilliham 2015 is a useful discussion of salinity tolerance in crops. Oh, et al. 2014 demonstrates how genome structural studies of the halophyte *Schrenkiella parvula* (formerly, *Thellungiella parvula*), a close relative of *Arabidopsis thaliana* and *Brassica* crop species, can shed light on genes underlying salt tolerance in plants. Salinity tolerance among other organisms has received less attention than that of plants. Although a little outdated, Kirst 1990 is the only available extensive treatment of salt tolerance in marine algae. Salt tolerance among aquatic invertebrates has also received some attention, shedding light on how rapid increases in salt in freshwater systems worldwide may be adversely affecting insect and other invertebrate diversity. Hassell, et al. 2006 employs laboratory studies to investigate levels of salinity tolerance among freshwater insects. Roberts 2004 reviews salinity tolerance of archaea in relation to what is known about osmoadaptation and osmoregulation in bacteria and eukaryotes, while Empadinhas and Costa 2008 provides an overview of osmoadaptation mechanisms in wide-ranging prokaryotes (see also Bakermans 2015, cited under General Overviews and Rampelotto 2013, cited under Major Stressors for additional coverage of bacterial adaptions to salinity). Salinity also represents a critical challenge to freshwater fishes and amphibians; Kültz 2015 and Hopkins and Brodie 2015 (cited under Evolutionary Aspects of Extremophiles) explore physiological mechanisms used by fishes and amphibians, respectively, to cope with salt and osmotic stress.

Empadinhas, Nuno, and Milton S. da Costa. 2008. Osmoadaptation mechanisms in prokaryotes: Distribution of compatible solutes. *International Microbiology* 11.3: 151–161.

The paper provides an overview of the diversity and distribution of known classes of compatible solutes used for osmoregulation by prokaryotes, as well as noting our increasing knowledge of the genes and pathways involved in their biosynthesis.

Flowers, Timothy J., and Timothy D. Colmer. 2015. Plant salt tolerance: Adaptations in halophytes. In *Special issue: Halophytes*. *Annals of Botany* 115.3: 327–331.

In this preface article to a special issue on halophytes and saline adaptations, the authors summarize our understanding of the evolution of salt tolerance in halophytes and their life-history traits, outlining new progress made on the molecular, biochemical, and physiological mechanisms contributing to salt tolerance.

Hassell, Kathryn L., Ben J. Kefford, and Dayanthi Nugegoda. 2006. Sub-lethal and chronic salinity tolerances of three freshwater insects: *Cloeon* sp. and *Centroptilum* sp. (Ephemeroptera: Baetidae) and *Chironomus* sp. (Diptera: Chironomidae). *Journal of Experimental Biology* 209.20: 4024–4032.

This study illustrates the variability in responses to increased salinity among insects, highlighting the need to investigate sublethal and chronic exposures in a range of freshwater invertebrates, in order to better predict the impacts of increasing salinity on freshwater biodiversity.

Kirst, Gunter O. 1990. Salinity tolerance of eukaryotic marine algae. *Annual Review of Plant Physiology and Plant Molecular Biology* 41:21–53.

An excellent introduction to salinity tolerance in marine algae, providing an overview of thresholds of salinity tolerance among algae species, morphological and physiological responses of algae to salt stress, processes of salt stress acclimation, and areas for future investigation.

Kültz, Dietmar. 2015. Physiological mechanisms used by fish to cope with salinity stress. *Journal of Experimental Biology* 218.12: 1907–1914.

The review examines the current state of knowledge of salinity tolerance among euryhaline fishes, including mechanisms that control dynamic changes in osmoregulatory strategy, from active salt absorption to salt secretion and from water excretion to water retention.

Munns, Rana, and Matthew Gilliham. 2015. Salinity tolerance of crops—what is the cost? *New Phytologist* 208.3: 668–673.

The authors explore mechanisms of adaptation to salt stress and highlight new advances in the applications of the underlying stress-tolerant traits to improve the energy efficiency of crops growing under salt-rich arable conditions.

Oh, Dong-Ha, Hyewon Hong, Sang Yeol Lee, Dae-Jin Yun, Hans J. Bohnert, and Maheshi Dassanayake. 2014. Genome structures and transcriptomes signify niche adaptation for the multiple-ion-tolerant extremophyte *Schrenkiella parvula*. *Plant Physiology* 164.4: 2123–2138.

The study shows that despite differences in adaptations to salinity, the genomes of close relatives, *S. parvula* and *Arabidopsis thaliana*, show extensive synteny. Comparative RNA sequencing shows enrichment of ion-transport functions among genes with higher expression in *S. parvula*, including increased copy number, higher transcript dosage, and evidence for subfunctionalization.

Roberts, Mary F. 2004. Osmoadaptation and osmoregulation in archaea: Update 2004. *Frontiers in Bioscience* 9 (1 September): 1999–2019.

This article provides an overview of responses of archaea to changes in salinity, including a comparison of mechanisms used for osmoadaptation and osmoregulation among archaea, bacteria, and eukaryotes.

Water Availability

Water makes up a significant fraction of the biomass of all organisms and is essential for maintaining structural, biochemical, and physiological attributes of life. However, extremes in water availability can cause severe physiological stress in all forms of biota. Habitats such as hot and cold deserts, rock outcrops, mountaintops, and saline and alkaline flats can be severely water-limiting due to soil physical (e.g., low water-holding capacity) or chemical (e.g., increased osmotic/ionic strength) features, while flooded habitats such as wetlands, swamps, bogs, and fens can experience physiological stress resulting from near-anaerobic soil conditions. Life exposed either to low or high water availability has adapted to those conditions via morphological, biochemical, and physiological means. For example, dehydration or desiccation tolerance is critical in habitats with low water availability (low water potential) or exceedingly high evapotranspiration, while the ability to generate sufficient energy for catabolic and anabolic processes is essential for tolerating waterlogged conditions. Water stress tolerance in plants has received much attention: Osakabe, et al. 2014 discusses molecular and physiological mechanisms associated with drought tolerance, while Kreuzwieser and Rennenberg 2014 offers excellent coverage of molecular and physiological responses to waterlogged conditions. Oliver, et al. 2005 takes a phylogenetic approach to understanding the evolution of desiccation tolerance in plants, showing that basic mechanisms of tolerance found in modern-day bryophytes have changed little from the earliest expressions of desiccation tolerance in land plants. Drought adaptations in microbes have also received much attention; Potts, et al. 2005 reviews the response of prokaryotic cells to desiccation and the mechanisms they employ to tolerate water stress at the level of the cell, genome, and proteome (see also Bakermans 2015, cited under General Overviews and Rampelotto 2013, cited under Major Stressors for additional coverage of bacterial adaptions to desiccation). Desiccation tolerance literature on fauna is more limited, however. Gibbs 2002 is a good source for adaptations to water stress in *Drosophila*, and Mizrahi, et al. 2010 is a similarly good source for land snails, while Tingaud-Sequeira, et al. 2013 investigates how killifish embryos are able to rapidly adjust to desiccation stress. Alpert 2005 is an excellent discussion of desiccation tolerance in a wide range of organisms, from prokaryotes to eukaryotes, exploring whether morphological and ecological limits to desiccation tolerance may be inherent, with phylogenetic limits to tolerance or physical or physiological constraints.

Alpert, Peter. 2005. The limits and frontiers of desiccation-tolerant life. *Integrative & Comparative Biology* 45.5: 685–695.

The review examines phylogenetic, physical, and physiological limits to desiccation tolerance in microbes, animals, and plants, demonstrating success in engineering tolerance in prokaryotes and in isolated cells and tissues and the lack of success in extending tolerance to whole, desiccation-sensitive multicellular animals and plants.

Gibbs, Allen G. 2002. Water balance in desert *Drosophila*: Lessons from non-charismatic microfauna. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 133.3: 781–789.

The author shows that desert fruit flies lose water less rapidly than their mesic congeners and that they are able to tolerate the loss of a greater percentage of body water. However, these differences are mainly due to phylogenetic history and do not represent specific adaptations to desert habitats.

Kreuzwieser, Jürgen, and Heinz Rennenberg. 2014. Molecular and physiological responses of trees to waterlogging stress. In *Special issue: Flooding and anaerobiosis*. *Plant, Cell & Environment* 37.10: 2245–2259.

The review summarizes physiological and molecular characteristics of waterlogging tolerance of trees, focusing on carbon metabolism in leaves and roots. A crucial feature of waterlogging tolerance is a steady supply of carbohydrates for glycolysis, particularly in the roots.

Mizrahi, Tal, Joseph Heller, Shoshana Goldenberg, and Zeev Arad. 2010. Heat shock proteins and resistance to desiccation in congeneric land snails. *Cell Stress and Chaperones* 15.4: 351–363.

The study demonstrates that land snails use heat shock proteins (HSPs) for survival during desiccation and as important components of the aestivation mechanism in the transition from activity to dormancy. Further, variations in the HSP response are documented both in timing and magnitude between desiccation-sensitive and desiccation-tolerant congeners.

Oliver, Melvin J., Jeff Velten, and Brent D. Mishler. 2005. Desiccation tolerance in bryophytes: A reflection of the primitive strategy for plant survival in dehydrating habitats? *Integrative & Comparative Biology* 45.5: 788–799.

The study suggests that desiccation tolerance is a primitive trait and that the adaptations by which the first land plants achieved tolerance are also found in extant desiccation-tolerant bryophytes. Further, it appears that vegetative desiccation tolerance in early land plants may have evolved from a mechanism first present in bryophyte spores.

Osakabe, Yuriko, Keishi Osakabe, Kazuo Shinozaki, and Lam-Son P. Tran. 2014. Response of plants to water stress. *Frontiers in Plant Science* 5 (13 March): 86.

Systems that regulate plant adaptation to water stress are the focus of this review. Molecular mechanisms that are used to increase water stress tolerance, maintain appropriate hormone homeostasis, and prevent excess light damage are also discussed. Moreover, how biotechnological advances can help improve drought tolerance in crops is addressed.

Potts, Malcolm, Stephen M. Slaughter, Frank-U. Hunneke, James F. Garst, and Richard F. Helm. 2005. Desiccation tolerance of prokaryotes: Application of principles to human cells. *Integrative & Comparative Biology* 45.5: 800–809.

The responses of the transcriptomes and proteomes of prokaryotic cells and eukaryotic cells (yeast and human) to desiccation are compared and contrasted to investigate whether there is a suite of structural, physiological, and molecular mechanisms that constitute desiccation tolerance in wide-ranging organisms.

Tingaud-Sequeira, Angèle, Juan-José Lozano, Cinta Zapater, et al. 2013. A rapid transcriptome response is associated with desiccation resistance in aerially-exposed killifish embryos. *PLoS ONE* 8.5: e64410.

The study documents transcriptional profiling of molecular processes associated with desiccation resistance during delayed hatching in killifish, showing that remarkable transcriptomic plasticity in the embryos allows for rapid tolerance of nonlethal desiccation conditions.

Oxygen

In aerobic organisms, oxygen is an absolute necessity for efficient production of ATP though oxidative phosphorylation. Depletion of oxygen has rapid and extreme consequences on cell physiology, altering gene expression, energy consumption, cellular metabolism, growth, and development. Stress caused by oxygen-limiting conditions can be chronic or short lived and can result from anoxia (i.e., absence of oxygen in the environment) as well as hypoxia (i.e., inadequate oxygen supply to tissue). All groups of aerobic organisms, from unicellular to multicellular, can experience anoxic and hypoxic conditions, leading to severe cellular and metabolic stress. Plants found under waterlogged conditions, such as wetlands, bogs, swamps, and rice paddies, often experience oxygen deprivation. Gibbs and Greenway 2003 is a good source for the literature on anoxia tolerance in plants, covering a range of topics relating to growth and survival under anoxic conditions. Bailey-Serres and Chang 2005 examines low-oxygen sensing and response mechanisms in wide-ranging organisms, including bacteria, fungi, metazoans, and plants, highlighting what is known of the underlying genetic basis of anoxia tolerance mechanisms in these groups. More-extensive coverage of the many types of anaerobic microbes is found in Ljungdahl, et al. 2003, which includes both general chapters and those that explore their biochemistry and physiology. Morris and Schmidt 2013 discusses microbes that are adapted to very low oxygen concentrations (microoxic conditions) and therefore operate along the borderline of aerobic and anaerobic conditions. Fago and Jensen 2015 reviews more-recent literature on anoxia tolerance in fish, turtles, and marine mammals, concluding that nitric oxide and nitrite play a critical role in tolerance to extreme oxygen deprivation. Scott 2011 examines the relative roles of adaptation versus acclimatization in tolerance to low oxygen among birds during high-altitude flight, documenting that both physiological and morphological traits are important in hypoxia tolerance. Seibel 2011 explores hypoxia in deep oceanic environments, highlighting physiological mechanisms associated with tolerance to oxygen-limiting zones in the ocean. Hochachka and Monge 2002 is a fascinating examination of the physiology of hypoxia tolerance among different human lineages, pointing out that both “conservative” and “adaptable” physiological traits are involved in human responses to hypoxia. The authors report that tolerance to high-altitude hypoxia may represent the human ancestral condition, consistent with late-20th-century evidence suggesting that humans evolved under cooler, drier, and high-elevation conditions in East Africa, where a hypoxia-tolerant phenotype would have been more beneficial for endurance performance.

Bailey-Serres, Julia, and Ruth Chang. 2005. Sensing and signalling in response to oxygen deprivation in plants and other organisms. *Annals of Botany* 96.4: 507–518.

The review focuses on mechanisms and processes of low-oxygen sensing and response in bacteria, fungi, metazoans, and plants, showing that multiple sensors and signal transduction pathways are involved in sensing oxygen deprivation. The underlying genetic bases for oxygen-sensing mechanisms and cellular responses to oxygen deprivation are also highlighted.

Fago, Angela, and Frank B. Jensen. 2015. Hypoxia tolerance, nitric oxide, and nitrite: Lessons from extreme animals. *Physiology* 30.2: 116–126.

This review highlights early-21st-century research documenting the important roles of nitric oxide and nitrite in tolerance to extreme oxygen deprivation, in particular in the red-eared slider turtle, crucian carp, and diving marine mammals.

Gibbs, Jane, and Hank Greenway. 2003. Review: Mechanisms of anoxia tolerance in plants I: Growth, survival and anaerobic catabolism. *Functional Plant Biology* 30.3:1–47.

The review discusses how plants deal with anoxia often experienced under waterlogged conditions, covering aspects of growth and survival, the interaction of anoxia tolerance with other environmental factors, the development of anoxic cores within plant tissues, anaerobic carbohydrate catabolism and its regulation, and mechanisms of post-anoxic injury.

Hochachka, Peter W., and C. Carlos Monge. 2002. Evolution of human hypoxia tolerance physiology. Paper presented at the XIVth International Symposium on Arterial Chemoreception, held 24–28 June 1999 in Philadelphia. In *Oxygen sensing: Molecule to man*. Edited by Sukhamay Lahiri, Nanduri R. Prabhakar, and Robert E. Forster II, 25–43. Advances in Experimental Medicine and Biology 475. New York: Kluwer Academic.

The authors summarize research on the physiology of hypoxia tolerance among different human lineages, including lowlanders, Andean natives, Himalayan natives, and East Africans, documenting both "conservative" and "adaptable" physiological traits involved in human responses to hypoxia.

Ljungdahl, Lars G., Michael W. Adams, Larry L. Barton, James G. Ferry, and Michael K. Johnson, eds. 2003. *Biochemistry and physiology of anaerobic bacteria*. New York: Springer.

The eighteen chapters in this edited volume provide entry to the literature about many features of anaerobic bacteria. Many chapters provide detailed explorations of the biochemical and physiological mechanisms that allow anaerobic microbes to operate in anoxic conditions.

Morris, Rachel L., and Thomas M. Schmidt. 2013. Shallow breathing: Bacterial life at low O_2. *Nature Reviews Microbiology* 11.3: 205–212.

Reviewing microbial adaptation to microoxic conditions (defined as extremely low oxygen concentrations), the authors summarize the phylogenetic and ecological distribution of these microbes and their roles in health and disease. These provide important contrasts both to aerobic and anaerobic bacteria.

Scott, Graham R. 2011. Elevated performance: The unique physiology of birds that fly at high altitudes. *Journal of Experimental Biology* 214.15: 2455–2462.

The review summarizes low-oxygen adaptations of high-flying birds, focusing on physiological and morphological traits associated with surviving oxygen-limiting environments. Specializations for efficient uptake, circulation, and utilization of oxygen during high-altitude hypoxia are highlighted, while acknowledging that the relative roles of adaptation and acclimatization in high-altitude flight are still unclear.

Seibel, Brad A. 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *Journal of Experimental Biology* 214.2: 326–336.

This is a good source for definitions of hypoxia and critical oxygen levels, adaptations of animals to oxygen minimum zones, responses to temporary hypoxia, and the possible consequences of climate change on oxygen-limiting oceanic environments.

Heavy Metals

Heavy metals are released into the environment both by anthropogenic and natural sources. Some heavy metals have important physiological roles in plants and other biota; however, high concentrations of these micronutrient metals or exposure to nonessential heavy metals can create physiological stress through interference with the function of proteins or with information-coding macromolecules, such as DNA or RNA. Heavy-metal-enriched habitats, both natural and man-made, therefore harbor organisms with adaptations to tolerate toxic metals. Heavy-metal-tolerant strains are found within all groups of microbes: Vishnivetskaya, et al. 2011 reports a mercury-tolerant bacterial community in streams exposed to surface water contamination, while Giller, et al. 2009 provides an excellent overview of how microbes are exposed to and respond to heavy metals in soils. Similar overviews are provided for lichens in Bačkor and Fahselt 2008, for fungi in Gadd 1993, and for insects in Janssens, et al. 2009. Heavy-metal tolerance can evolve rapidly: the section on genetics and evolution in the *Oxford Bibliographies* in Ecology article on "Heavy Metal Tolerance" provides an overview of this topic. There is extensive research on the physiological and genetic aspects of metal tolerance in plants: for a broad overview, see Bothe 2011. Metal-hyperaccumulating plants, those that take up greater than 0.1 percent of their dry weight in a metal, are found on serpentine (ultramafic) rock outcrops and in other metal-enriched soils and have been the subject of intense investigation in the early 21st century. Van der Ent, et al. 2013 provides extensive coverage on metal hyperaccumulation in plants, while the section on coevolutionary relationships in the *Oxford Bibliographies* in Ecology article "Heavy Metal Tolerance" discusses ecological and evolutionary aspects of other biota, particularly insects and mycorrhizal fungi, associated with plants that accumulate heavy metals. Gall, et al. 2015 reviews how heavy metals enter soils and groundwater, bioaccumulate in organisms, transfer across trophic levels, and can adversely affect microbes, plants, invertebrates, small mammals, and large mammals (including humans).

Bačkor, Martin, and Dianne Fahselt. 2008. Lichen photobionts and metal toxicity. *Symbiosis* 46.1: 1–10.

In a lichen, symbiotic algae or cyanobacterial partners (photobionts) and their associated fungi (mycobionts) can be sensitive to heavy-metal stress. The review focuses on biochemical and physiological mechanisms relating to heavy-metal tolerance in lichens, documenting that metal tolerance depends on the metal, its concentration, and the strain of photobiont.

Bothe, Hermann. 2011. Plants in heavy metal soils. In *Detoxification of heavy metals*. Edited by Irena Sherameti and Ajit Varma, 35–57. Soil Biology 30. Berlin: Springer-Verlag.

This is an excellent gateway to the literature on plant heavy-metal tolerance, providing good coverage of the physiological and biochemical mechanisms employed by plants to tolerate heavy metals. The article also extends into applied uses of metal-tolerant plants in phytoremediation situations.

Gadd, Geoffrey M. 1993. Interactions of fungi with toxic metals. *New Phytologist* 124.1: 25–60.

This review focuses on mechanisms of heavy-metal toxicity in fungi, including resistance and tolerance to metals brought about by biochemical and physiological processes at the cellular and extracellular levels. Significant interactions between heavy metals and mycorrhizal fungi and macrofungi are summarized, including environmental influences on metal toxicity in fungi.

Gall, Jillian E., Robert S. Boyd, and Nishanta Rajakaruna. 2015. Transfer of heavy metals through terrestrial food webs: A review. *Environmental Monitoring and Assessment* 187.4: 201.

The review provides extensive coverage on the effects of heavy metals on plants and associated biota (soil invertebrates, insects, small mammals, large mammals, and humans), including the environmental and toxicological impacts of metal transfer across trophic levels.

Giller, Ken E., Ernst Witter, and Steve P. McGrath. 2009. Heavy metals and soil microbes. *Soil Biology and Biochemistry* 41.10: 2031–2037.

The review addresses advances in the study of toxicology of metals and their effects on soil organisms, highlighting major gaps in our understanding of microbe-metal interactions and discussing the need for long-term experiments and basic research to establish relevant environmental-protection policies and enhance knowledge of microbe-metal relations.

Janssens, Thierry K. S., Dick Roelofs, and Nico M. van Straalen. 2009. Molecular mechanisms of heavy metal tolerance and evolution in invertebrates. *Insect Science* 16.1: 3–18.

The review focuses on metal tolerance in insects and other invertebrates, highlighting then-recent work on metallothioneins and how their overexpression promotes cadmium tolerance in springtails (Collembola).

van der Ent, Antony, Alan J. M. Baker, Roger D. Reeves, A. Joseph Pollard, and Henk Schat. 2013. Hyperaccumulators of metal and metalloid trace elements: Facts and fiction. *Plant and Soil* 362 (January): 319–334.

This review discusses the circumstances in which the term “hyperaccumulator” is appropriate, outlining the conditions to be met when the term is used. It summarizes the main considerations for establishing metal hyperaccumulation in plants and redefines previous terminology, including thresholds for the hyperaccumulation of various metals.

Vishnivetskaya, Tatiana A., Jennifer J. Mosher, Anthony V. Palumbo, et al. 2011. Mercury and other heavy metals influence bacterial community structure in contaminated Tennessee streams. *Applied and Environmental Microbiology* 77.1: 302–311.

The study employs genetic methods to characterize the bacterial community of metal-contaminated surface stream sediments, finding significant correlations between the bacterial community and seasonal and geochemical factors, including several strains positively associated with mercury (Hg) and methylmercury (MeHg).

Polyextremophiles

Organisms that inhabit environments influenced by more than one abiotic stress are known as polyextremophiles. Seckbach, et al. 2013 is an authoritative treatment of multiple stress tolerance among prokaryotic and eukaryotic microbes, green algae, and fungi from habitats characterized by high or low temperature, desiccation, acidic or alkaline conditions, hypersalinity, high pressure, toxic compounds, high levels of radiation, anoxia, and the absence of light, among other abiotic stresses. Much attention has been paid to polyextremophile microbes, the organisms most often studied for multiple stress tolerances. Harrison, et al. 2013 explores the boundaries for microbial life under a combination of stresses, including temperature, salinity, pressure, and pH, and reviews what is known about the underlying adaptations to multiple abiotic stresses. Bowers, et al. 2009 discusses anaerobic, halophilic, alkalithermophilic microbes (those tolerant of low oxygen, high salt, pH, and temperature) and how their adaptive mechanisms provide insight into how organisms can survive in environments that were previously considered uninhabitable by life. Selby, et al. 2014 (cited under Evolutionary Aspects of Extremophiles) summarizes multiple stress tolerance in the model plant *Mimulus*, reviewing quantitative trait loci mapping, high-throughput phenotyping, and population genomic methods alongside field- and lab-based assays used to explore the genetic architecture of phenological (i.e., flowering-time) escape from seasonal drought and soils enriched with heavy metals and salt. Von Wettberg, et al. 2014 discusses similarities in plant stress resistance syndrome traits across harsh environments, suggesting that adaptations to extreme habitats share common physiological mechanisms and a common molecular basis. Zwack and Rashotte 2015 reviews hormones as key regulators of multiple stress tolerance in plants, particularly the role of specific cytokinin-signaling components in the response to a variety of abiotic stressors. An understanding of the underlying physiological and genetic basis for multiple stress tolerance is vital for agricultural applications; Qin, et al. 2015 identifies TaWRKY93, a new positive regulator of abiotic stress in wheat, which increases salinity, drought, and cold-stress tolerance through enhancing osmotic adjustment, maintaining membrane stability, and increasing transcription of stress-associated genes. Such studies are essential for breeding transgenic crops tolerant of combined abiotic and biotic stresses, as also emphasized in Kissoudis, et al. 2014. The importance of studying the physiological basis of responses to climate change is another important topic reviewed in Bozinovic and Pörtner 2015, showing that the study of tolerance limits to multiple stressors both on land and in water is vital for understanding climate change impacts on organisms.

Bowers, Karen J., Noha M. Mesbah, and Juergen Wiegel. 2009. Biodiversity of poly-extremophilic *Bacteria*: Does combining the extremes of high salt, alkaline pH and elevated temperature approach a physico-chemical boundary for life? *Saline Systems* 5:9.

The review discusses the diversity of extremophilic microbes and their physiological and biochemical properties, including their known tolerance limits to abiotic stresses such as salt, pH, and temperature. The use of polyextremophilic bacterial halophiles in biotechnological applications is also highlighted.

Bozinovic, Francisco, and Hans-Otto Pörtner. 2015. Physiological ecology meets climate change. *Ecology and Evolution* 5.5: 1025–1030.

The importance of understanding the physiology of differential climate change effects on organisms within and across domains (Archaea, Bacteria, and Eukarya) is the topic of this review. A unified experimental approach is outlined for projecting future ecological and evolutionary effects of climate change on whole organisms and ecosystem functioning.

Harrison, Jesse P., Nicolas Gheeraert, Dmitry Tsigelnitskiy, and Charles S. Cockell. 2013. The limits for life under multiple extremes. *Trends in Microbiology* 21.4: 204–212.

The authors discuss the limitations for microbial life under combined extremes of temperature, pH, salt, and pressure, suggesting that a lack of information on microbial tolerance to multiple abiotic stresses can impede advances in environmental and industrial microbiology and the search for extraterrestrial life.

Kissoudis, Christos, Clemens van de Wiel, Richard G. F. Visser, and Gerard van der Linden. 2014. Enhancing crop resilience to combined abiotic and biotic stress through the dissection of physiological and molecular crosstalk. *Frontiers in Plant Science* 5:207.

The authors discuss molecular components with potentially critical roles in abiotic and biotic stress tolerance in plants and propose breeding approaches toward effective crop improvement against combinatorial stress. Insights on stress cross regulation and candidate genes for improving crop performance under combined stress are also highlighted.

Qin, Yuxiang, Yanchen Tian, and Xiuzhi Liu. 2015. A wheat salinity-induced WRKY transcription factor TaWRKY93 confers multiple abiotic stress tolerance in *Arabidopsis thaliana*. *Biochemical and Biophysical Research Communications* 464.2: 428–433.

The paper describes TaWRKY93, a then recently discovered positive regulator of abiotic stress, as vital to increasing tolerance to salinity, drought, and low temperature in wheat. Its role as a candidate gene for breeding transgenic wheat tolerant of multiple abiotic stresses is also discussed.

Seckbach, Joseph, Aharon Oren, and Helga Stan-Lotter, eds. 2013. *Polyextremophiles: Life under multiple forms of stress*. Cellular Origin, Life in Extreme Habitats and Astrobiology 27. Dordrecht, The Netherlands: Springer.

This authoritative treatment on polyextremophiles consists of thirty chapters covering wide-ranging topics relating to the diversity, physiology, and evolution of organisms tolerant of extremes in salinity, pH, radiation, temperature, and anoxia, among other abiotic variables. The applications of polyextremophile research in nanotechnology, synthetic biology, and astrobiology are also discussed.

von Wettberg, Eric J. B., Jayanti Ray-Mukherjee, Nathan D'Adesky, Damian Nesbeth, and Seeta Sistla. 2014. The evolutionary ecology and genetics of stress resistance syndrome (SRS) traits: Revisiting Chapin, Autumn and Pugnaire (1993). In *Plant ecology and evolution in harsh environments*. Edited by Nishanta Rajakaruna, Robert S. Boyd, and Tanner B. Harris, 201–226. Environmental Research Advances. Hauppauge, NY: Nova Science.

The authors discuss how plants in stressful habitats share a suite of traits, or a stress resistance syndrome, that provides broad adaptation across several harsh environments. They outline how studies in phylogenomics, population genomics, developmental genetics, and comparative biology are vital for understanding the stress resistance syndrome in nonmodel plants.

Zwack, Paul J., and Aaron M. Rashotte. 2015. Interactions between cytokinin signalling and abiotic stress responses. *Journal of Experimental Botany* 66.16: 4863–4871.

The authors address the role of plant hormones as key regulators of multiple stress tolerance, connecting local stimuli to systemic responses. The physiological relationship between cytokinin and abiotic stress, on the basis of measurements of cytokinin levels under stress and the effects of cytokinin treatment on stress tolerance, is also discussed.

Broad Themes

Extreme environments provide habitats for organisms able to thrive under conditions inhospitable for others. Such environments often provide model settings to explore the evolutionary process driven by adaptations to extreme abiotic conditions (see Evolutionary Aspects of Extremophiles). Many extreme environments are under threat from anthropogenic disturbances and are in need of conservation because they are home to a disproportionately high percentage of rare and endemic species (see Conservation of Extreme Environments). Additionally, organisms living in such environments can be overly influenced by global climate change, including changes in temperature and water availability, because their survival and competitiveness necessitate tolerance to narrow thresholds of abiotic stressors (see Climate Change and Extreme Environments). Rapid climatic changes can lead to extinctions if the extremophiles are not climate resistant, cannot compete outside their narrow climatic tolerance regime, or are unable to disperse into favorable niches; their survival often will depend on how quickly and how far they can disperse in order to reach their favored habitats. Restoration of extremophile habitats is also receiving attention because these habitats continue to be adversely affected by human and natural disturbances, and the organisms that are locally adapted to the abiotic stressors characterizing their habitats are under threat from extinction (see Restoration of Extreme Environments). Finally, an understanding of the genetic basis for stress tolerance in organisms found in extreme environments can provide innovative solutions to many industrial, agricultural, medical, environmental, and other biotechnological problems (see Applied Uses of Extremophiles).

Evolutionary Aspects of Extremophiles

Environments with extreme physicochemical conditions often contain rare and endemic species. Such harsh habitats with their uniquely adapted biota have naturally aroused great interest among evolutionary ecologists. Hlodan 2010 provides a broad sampling of current research on adaptive evolution in some of the world's harshest environments. Extreme environments, including extremes in temperature, radiation, substrate salinity, oxygen, pH, nutrients, and heavy metals, can provide prime settings in which to examine the factors and mechanisms driving the evolutionary process. Some of the earliest evidence for adaptive evolution in plants came from studies of plants growing in extreme habitats such as metal-rich mine tailings (see *Oxford Bibliographies* article Heavy Metal Tolerance section "Plants") and serpentine outcrops (see the section on evolutionary aspects in the *Oxford Bibliographies* in Ecology article "Serpentine Soils"). Selby, et al. 2014 is an excellent review of how early-21st-century developments in genomic approaches are driving further advances in understanding the genetics of adaption and speciation under stress in the model plant genus *Mimulus*. Organisms in extreme environments either have genotypes broadly tolerant to wide-ranging environmental conditions or are habitat specialists adapted to the particular biotic and abiotic stressors that characterize their environment. Von Wettberg, et al. 2014 (cited under Polyextremophiles) is an excellent discussion of how organisms respond to stress, examining whether extremophiles share a suite of traits, or a stress resistance syndrome, that provide broad adaptation across a range of extreme habitats. The authors also summarize an array of molecular tools available to study the genetics of divergence under stress. Rajakaruna, et al. 2014 is a good overview of the role played by extreme environments in the origin of new species, particularly in plants. Using case studies of edaphically specialized plants, O'Dell and Rajakaruna 2011 shows that habitat specialists arise via two mechanisms: neoendemics, arising from nearby, nonspecialized relatives via rapid and local speciation, or paleoendemics, resulting from gradual speciation via biotype depletion; similar modes of evolution can be seen across distinct life forms and different extreme environments. Gostinčar, et al. 2010 examines fungal evolution under ice and salt stress, showing that preadaptations facilitate persistence and eventual adaptation to conditions on the ecological edge, including the evolution of new biotypes. Saslis-Lagoudakis, et al. 2014 investigates evolutionary patterns of salt tolerance in plants via phylogenetic analyses, exploring evolutionary associations between salt tolerance and other related ecophysiological strategies. Cheeseman 2015 is an outstanding review on the evolution of halophytes, including implications of current research to developing salt-tolerant crops. Hopkins and Brodie 2015 provides a good overview of the evolutionary processes leading to salinity adaptation in amphibians. Riesch, et al. 2015 (cited under General Overviews) summarizes the key adaptations enabling the evolution of extremophile fishes under harsh aquatic conditions, pointing out generalities that are found across different study systems.

Cheeseman, John M. 2015. The evolution of halophytes, glycophytes and crops, and its implications for food security under saline conditions. *New Phytologist* 206.2: 557–570.

The author discusses halophyte evolution both at the ecological and genomic levels, including aspects of the evolution of glycophytes and the evolution/domestication of crop species. Experimental approaches to understanding halophyte evolution and for development of salt-tolerant crops on the basis of evolutionary precedents are also reviewed.

Gostinčar, Cene, Martin Grube, Sybren de Hoog, Polona Zalar, and Nina Gunde-Cimerman. 2010. Extremotolerance in fungi: Evolution on the edge. *FEMS Microbiology Ecology* 71.1: 2–11.

An excellent review of early-21st-century studies of extremophile fungi, including a discussion of mechanisms allowing adaptation under stress. Traits present in some fungi, such as asexuality, synthesis of melanin-like pigments, and a flexible morphology, are suggested as preadaptations for cross-tolerance to multiple stresses, facilitating the evolution of habitat specialization.

Hlodan, Oksana. 2010. Evolution in extreme environments. *BioScience* 60.6: 414–418.

Based on the "Evolution in Extreme Environments" symposium of the 2009 National Association of Biology Teachers professional development conference, this article illustrates that adaptations of humans to high altitudes, of sea jellies to the deep sea, of cavefishes to sunless caves, and of microbes to Arctic winter ice demonstrate processes of adaptive evolution in harsh environments.

Hopkins, Gareth R., and Edmund D. Brodie Jr. 2015. Occurrence of amphibians in saline habitats: A review and evolutionary perspective. *Herpetological Monographs* 29:1–27.

A review highlighting literature regarding amphibians in saline waters, suggesting that salt tolerance in amphibians may not be as rare as previously assumed. An excellent summary of existing knowledge, and an insightful discussion of a possible framework toward the development of an evolutionary model of amphibian adaptation to salinity.

O'Dell, Ryan E., and Nishanta Rajakaruna. 2011. Intraspecific variation, adaptation, and evolution. In *Serpentine: Evolution and ecology of a model system*. Edited by Susan Harrison and Nishanta Rajakaruna, 97–137. Berkeley: Univ. of California Press.

An extensive treatment on the evolution of plants adapted to serpentine and other extreme edaphic settings, highlighting functional-trait differences between close relatives found on contrasting substrates and what is known about adaptations and modes of evolution under edaphic stresses.

Rajakaruna, Nishanta, Robert S. Boyd, and Tanner B. Harris. 2014. Synthesis and future directions: What have harsh environments taught us about ecology, evolution, conservation and restoration? In *Plant ecology and evolution in harsh environments*. Edited by Nishanta Rajakaruna, Robert S. Boyd, and Tanner B. Harris, 393–409. Environmental Research Advances. Hauppauge, NY: Nova Science.

The concluding chapter of a book on the ecology and evolution of extremophiles, from microbes to higher plants, is an ideal gateway into understanding what harsh environments have taught us about adaptation, speciation, and community assembly in habitats characterized by extremes in abiotic conditions.

Saslis-Lagoudakis, C. Haris, Camile Moray, and Lindell Bromham. 2014. Evolution of salt tolerance in angiosperms: A phylogenetic approach. In *Plant ecology and evolution in harsh environments*. Edited by Nishanta Rajakaruna, Robert S. Boyd, and Tanner B. Harris, 77–96. Environmental Research Advances. Hauppauge, NY: Nova Science.

The chapter highlights a phylogenetic comparative analytical approach in exploring the evolutionary associations between salt tolerance and related ecophysiological strategies: C_4 photosynthesis, metal tolerance, and alkali tolerance. Such approaches are useful in assessing the evolutionary dynamics of stress tolerance, including in the identification of shared mechanisms underlying tolerance to multiple stresses.

Selby, Jessica P., Annie L. Jeong, Katherine Toll, Kevin M. Wright, and David B. Lowry. 2014. Methods and discoveries in the pursuit of understanding the genetic basis of adaptation to harsh environments in *Mimulus*. In *Plant ecology and evolution in harsh environments*. Edited by Nishanta Rajakaruna, Robert S. Boyd, and Tanner B. Harris, 243–266. Environmental Research Advances. Hauppauge, NY: Nova Science.

Early-21st-century studies on the tolerance to drought, serpentine, copper, and salinity in the genus *Mimulus* highlight insights into the mechanisms of adaptation and speciation. High-throughput phenotyping and other genomic methods are described to show how novel molecular tools can reveal the genetic basis of adaptive evolution in harsh environments.

Conservation of Extreme Environments

Although organisms tolerant of environmental extremes are relatively tough, they still need conservation protection. In some cases this is because human disturbance can change environmental conditions to less extreme ones that these specialized organisms cannot tolerate, whereas in other cases human activity directly or indirectly destroys organisms and their habitat. One reason to conserve organisms inhabiting extreme environments is their value in biotechnology (see Applied Uses of Extremophiles); another is because they have important functions in communities and ecosystems. As an example of both reasons, Meckenstock, et al. 2014 describes anaerobic microorganism communities from the world's largest asphalt lake. These microorganisms form distinctive communities and may have unique abilities to biodegrade oil pollution. Some extreme environments have been impacted by humans for many centuries: these include special soil types, such as serpentine soils, that are associated with valuable metal ores. O'Dell 2014 provides a detailed overview of the conservation of extreme soil floras in the western United States, where mining is one of many threats. Many extreme environments (deserts, deep oceans, tundra, etc.) have been relatively safe from human disruption, but modern technological advances and the global impacts of humans are allowing previously pristine habitats to be affected. As an example, Van Dover 2014 discusses potential impacts of humans on deep-sea vent ecosystems: these impacts include impending deep-sea hydrothermal-vent mining projects that are now becoming economically and technologically feasible. Similarly, Hughes, et al. 2015 discusses conservation challenges in Antarctica, where many unique bacterial communities and habitats are found but conservation protection by the Antarctic Treaty is inadequate. Specific extreme habitats often have information sources devoted specifically to their conservation. Malloy, et al. 2013 discusses development in the American Southwest and suggests new approaches to planning, design, and building that will better conserve desert ecosystems, while Siikamäki, et al. 2012 considers strategies for conserving Earth's rapidly disappearing mangrove forests (which thrive in relatively extreme salinity conditions). Conservation concerns even extend to space exploration: one reason we attempt to keep space vehicles sterile is so that we do not introduce Earth's biota to other planets (where it may negatively affect native life forms). This attempt at "planetary protection" is daunting: Vaishampayan, et al. 2013 reports that bacteria are found even in spacecraft assembly "clean rooms," and Dadachova and Casadevall 2008 (cited under Radiation) points out that fungi have been found in orbiting spacecraft.

Hughes, Kevin A., Don A. Cowan, and Annick Wilmotte. 2015. Protection of Antarctic microbial communities—"out of sight, out of mind." *Frontiers in Microbiology* 6:151.

The authors consider microbial communities in Antarctica: rich in endemic extremophiles and faced with increasing levels of human activities. They discuss the inadequacy of current international agreements and propose future steps needed to ensure biodiversity protection. These steps may provide a model for conservation in other extreme habitats.

Malloy, Richard, John Brock, Anthony Floyd, Margaret Livingston, and Robert H. Webb, eds. 2013. *Design with the desert: Conservation and sustainable development*. Boca Raton, FL: CRC.

This edited book contains thirty-one chapters, starting with a review of desert environments, their resources, and conservation challenges. Additional chapters deal with many issues of planning and development, suggesting changes that will make human communities more sustainable and protect the desert's biota.

Meckenstock, Rainer U., Frederick von Netzer, Christine Stumpp, et al. 2014. Water droplets in oil are microhabitats for microbial life. *Science* 345.6197: 673–676.

The authors find microorganisms inhabiting tiny water droplets entrapped in the oil of an asphalt lake. The droplets contained complex microbial communities of bacteria and archaea that were metabolizing the oil.

O'Dell, Ryan E. 2014. Conservation and restoration of chemically extreme edaphic endemic flora in the western US. In *Plant ecology and evolution in harsh environments*. Edited by Nishanta Rajakaruna, Robert S. Boyd, and Tanner B. Harris, 313–364. Environmental Research Advances. Hauppauge, NY: Nova Science.

An excellent detailed case study of conservation and restoration issues involving plant species inhabiting extreme soils in this region, the paper examines the legal status of species and protected areas and discusses future conservation challenges to these special areas.

Siikamäki, Juha, James N. Sanchirico, and Sunny L. Jardine. 2012. Global economic potential for reducing carbon dioxide emissions from mangrove loss. *Proceedings of the National Academy of Sciences of the United States of America* 109.36: 14369–14374.

This article examines the feasibility of protecting salt-tolerant mangrove forests on the basis of their value for protecting the planet from carbon emissions. The authors suggest that this function may aid mangrove conservation programs, although many other conservation challenges must also be considered.

Vaishampayan, Parag, Christine Moissl-Eichinger, Rüdiger Pukall, et al. 2013. Description of *Tersicoccus phoenicis* gen. nov., sp. nov. isolated from spacecraft assembly clean room environments. *Journal of Systematic and Evolutionary Microbiology* 63.7: 2463–2471.

Illustrating the ability of some bacteria to live in extreme environmental conditions, the authors isolate a new bacterial genus from the floor of two facilities that had been rigorously cleaned in order to prevent introducing Earth organisms onto spacecraft during assembly.

Van Dover, Cindy Lee. 2014. Impacts of anthropogenic disturbances at deep-sea hydrothermal vent ecosystems: A review. In *Special issue: Managing biodiversity in a changing ocean*. *Marine Environmental Research* 102 (December): 59–72.

This review evaluates impacts of human activities at a classic extremophile habitat. The author highlights our current knowledge of natural and human disturbances to these ecosystems, as well as the many knowledge gaps, and discusses potential strategies for mitigation that might allow commercial exploitation to be balanced by biodiversity protection.

Climate Change and Extreme Environments

Changing climatic conditions, such as new terrestrial and aquatic temperature extremes, increased frequency of natural disasters, and shifts in atmospheric chemical composition, all pose serious threats to life on Earth. Some changes are caused by humans while others are due to natural phenomena. Regardless, the vast majority of scientists agree that climate change is occurring. Yet, a gap exists in our understanding of the broader, biological implications for organisms in extreme environments. To predict the impact of climate change, cross-disciplinary and combinational approaches are needed since reductionistic approaches can control only a limited number of factors. For example, Reyer, et al. 2013 uses a combination of quantitative-modeling, observational, and experimental approaches to assess the impacts of increasingly variable and extreme climatic conditions on plant species and communities. Similarly, Hinzman, et al. 2005 addresses the complexity of climate change impacts (such as warming permafrost and altered hydrological processes in the Arctic) by using a holistic approach. Baseline knowledge for understanding the response of species and communities to global environmental change requires an understanding of species' range limits and the plasticity of their responses to environmental extremes. Sinclair, et al. 2003 reviews strategies and adaptations for insect cold hardiness, and the implications of this knowledge for changing abiotic conditions. Due to the increasing amplitude of environmental extremes and record-breaking conditions, considerations of the biological implications of extreme conditions are becoming widespread. For example, Zimmermann, et al. 2009 demonstrates the importance of using climate extremes (in addition to mean values) in modeling the impact of abiotic variables on distribution of tree species in Switzerland. Not all regions will be affected by climate change in the same manner. Smol and Douglas 2007 highlights the susceptibility of surficial waters in Arctic regions, which are biodiversity hotspots, to increased evaporation/precipitation ratios stemming from warming conditions. Similarly, Peck, et al. 2004 stresses the sensitivity of Antarctic marine species to warming conditions by using species-specific analyses of physiological capacity and responses to increasingly hypoxic and lethal upper temperature conditions. The susceptibility of Antarctic Dry Valleys to climate change is of interest for their similarity to Mars's environment, as highlighted in Marchant and Head 2007. Important research gaps exist in our understanding of climate change impacts on biotic communities in extreme environments: better understanding of the structure, function, and susceptibility of extreme environments to climate change is needed to assess climate change impacts on organisms occupying extreme habitats.

Hinzman, Larry D., Neil D. Bettez, W. Robert Bolton, et al. 2005. Evidence and implications of recent climate change in northern Alaska and other Arctic regions. *Climatic Change* 72.3: 251–298.

This paper evaluates climatic changes affecting the Arctic, arguing that system-wide response to altered and extreme climatic conditions is occurring. Both criticized and well received for its interdisciplinary holistic approach, it suggests coupling large-scale experimental studies with remote sensing, modeling, and other novel technologies.

Marchant, David R., and James W. Head III. 2007. Antarctic Dry Valleys: Microclimate zonation, variable geomorphic processes, and implications for assessing climate change on Mars. *Icarus* 192.1: 187–222.

This paper examines climate change impacts for Antarctic Dry Valleys, hyperarid yet cold polar deserts, which resemble the climate and surficial features of Mars. Understanding this extreme environment has become of interest as a proxy for evaluating Mars's past, present, and future climate.

Peck, Lloyd S., Karen E. Webb, and David M. Bailey. 2004. Extreme sensitivity of biological function to temperature in Antarctic marine species. *Functional Ecology* 18.5: 625–630.

The authors examine the effects of increased ocean temperature, specifically loss of aerobic capacity, on Antarctic marine species (such as mollusks, limpets, and scallops), and suggest that even a 2°C rise in ocean temperature could result in species or population loss in the Southern Ocean.

Reyer, Christopher P. O., Sebastian Leuzinger, Anja Rammig, et al. 2013. A plant's perspective of extremes: Terrestrial plant responses to changing climatic variability. *Global Change Biology* 19.1: 75–89.

The authors employ a combined approach using observational, experimental, and modeling studies to investigate plant response to extreme conditions induced by climate change. They stress the importance of integrating these techniques as well as analyzing results with consideration to temporal scale and the inherent variability of the system studied.

Sinclair, Brent J., Philippe Vernon, C. Jaco Klok, and Steven L. Chown. 2003. Insects at low temperatures: An ecological perspective. *Trends in Ecology & Evolution* 18.5: 257–262.

This review provides a broad look at insect response to low temperature extremes, by using mechanistic, genomic, and modeling approaches, and suggests that improving current understanding of insect cold hardiness will shed light on insect distribution and population variability triggered by a changing climate.

Smol, John P., and Marianne S. V. Douglas. 2007. Crossing the final ecological threshold in high Arctic ponds. *Proceedings of the National Academy of Sciences of the United States of America* 104.30: 12395–12397.

The impact of climate change on high-latitude polar regions is often understudied despite their high sensitivity to warming conditions due to positive feedback loops. Using paleolimnological data, the authors demonstrate that Arctic ponds are becoming completely desiccated over the summer and thus have crossed a final ecological threshold.

Zimmermann, Niklaus E., Nigel G. Yoccoz, Thomas C. Edwards, et al. 2009. Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences of the United States of America* 106.S2: 19723–19728.

Using general additive models, this paper demonstrates the value of using climatic extremes to predict spatial limits of tree species in Switzerland under future conditions. As the frequency of climatic extremes increases, it is most effective to use extreme and mean values of environmental variables to predict species' distribution shifts.

Restoration of Extreme Environments

Ecological restoration is recovery of at least some portion of the original biota and ecological functionality of an ecosystem. Its importance is growing as Earth's burgeoning human population and our rapidly advancing technology increasingly threaten our planet's biological systems. Van Andel and Aronson 2006 provides a good introduction to the principles and practices of ecological restoration, many of which pertain to extreme environments. In general, however, restoration of communities and ecosystems in extreme environments is more difficult than in other environments, due to the challenges of working with specialized species under harsh conditions that slow rates of recovery. Some extreme environments (e.g., deserts, salt marshes, habitats underlain by metal-ore-bearing rocks) have been adversely affected by humans for millennia. *Oxford Bibliographies* in Ecology article "Geoecology, specifically the section on reclamation and restoration, provides an overview of the difficulties of ecological restoration of plant communities on soils derived from chemically unusual rocks. Bainbridge 2007 covers the extensive literature regarding restoration of desert communities, while Naeth and Wilkinson 2014 is a case study on restoring Arctic tundra disturbed by mining. Copson and Whinam 2001 is an interesting case study of ecological restoration on an Antarctic island that illustrates how complicated the control of non-native species can be: in that case, control of one species (feral rabbits) led to increased damage by feral cats and the spread of rats. Salt marshes are another extreme environment seriously affected by humans and now subject to widespread restoration attempts. Gedan, et al. 2009 reviews human impacts on salt marshes and discusses restoration, conservation, and management of these important coastal ecosystems. In contrast to these examples, restoration of other extreme habitats is only now being contemplated because technology is allowing human disturbance to become a serious challenge. For example, Van Dover, et al. 2014 discusses restoration of deep-sea habitats, especially those that may be the targets of deep-sea mining projects, pointing out the huge knowledge gaps that hamper effective planning, as well as other constraints such as much-greater costs of restoration in these remote locations.

Bainbridge, David A. 2007. *A guide for desert and dryland restoration: New hope for arid lands*. Science and Practice of Ecological Restoration. Washington, DC: Island.

This book provides an excellent overview of the techniques that can be used to restore damaged dryland habitats. The book emphasizes practical approaches and describes how to evaluate, plan, implement, and gauge the success of restoration projects in arid habitats.

Copson, Geof, and Jennie Whinam. 2001. Review of ecological restoration programme on subantarctic Macquarie Island: Pest management progress and future directions. *Ecological Management & Restoration* 2.2: 129–138.

A fascinating case study in which managers were faced with the need to control several exotic animal species. They show the importance of monitoring during restoration, as new problems raised by control measures required new management actions to continue recovery of native species.

Gedan, Keryn Bromberg, Brian R. Silliman, and Mark D. Bertness. 2009. Centuries of human-driven change in salt marsh ecosystems. *Annual Review of Marine Science* 1:117–141.

An excellent global review that documents the many human impacts on salt marsh habitats and the ecological changes they produce. The authors also evaluate conservation and restoration approaches, making this a good gateway to the literature regarding this extreme environment.

Naeth, M. Anne, and Sarah R. Wilkinson. 2014. Establishment of restoration trajectories for upland tundra communities on diamond mine wastes in the Canadian Arctic. *Restoration Ecology* 22.4: 534–543.

The authors experimentally manipulate several factors as they test restoration effectiveness. They find that several treatments enhanced success but that restoration was slowed by the harsh environment, and conclude that only long-term studies can effectively assess restoration techniques.

van Andel, Jelte, and James Aronson, eds. 2006. *Restoration ecology: The new frontier*. Malden, MA: Blackwell Science.

An excellent overview of this new field, the book covers the concepts and ecological principles that underlie restoration ecology. It also has eight chapters covering restoration of particular types of freshwater and terrestrial communities.

Van Dover, Cindy Lee, James Aronson, Linwood Pendleton, et al. 2014. Ecological restoration in the deep sea: Desiderata. *Marine Policy* 44 (February): 98–106.

This paper presents a thorough consideration of the issues underlying ecological restoration of deep-sea habitats. It presents two case studies estimating the cost of ecological restoration of these habitats, finding they may be two to three orders of magnitude greater than ecological restoration of shallow-water marine habitats.

Applied Uses of Extremophiles

Extremophiles, especially prokaryotes, are receiving extensive interest for their applied uses. Extremophiles are sources of bioactive compounds, can be used directly in industrial processes, and contain genes that can be used to modify traits of other organisms (genetic engineering). As an example of the last phenomenon, Pan, et al. 2009 (cited under Radiation) describes that a gene involved in radioresistance of an extremophile conferred salinity tolerance on the bacterium *Escherichia coli* and rapeseed (a crop plant). The unique physiology of extremophiles often produces compounds not found in organisms inhabiting less extreme environments. Giddings and Newman 2015 is one of several short books by Lesley-Ann Giddings and David Newman about extremophiles from various environments: this book catalogues compounds discovered from extremophiles in marine environments and illustrates their potential medical and biotechnological uses. Singh 2013 covers many applied uses of extremophiles and highlights the usefulness of extremophiles that tolerate oxygen, temperature, pH, and radiation extremes, among others. Similarly, Anitori 2012 presents extensive information on biotechnological uses of a wide variety of extremophiles, and Dalmaso, et al. 2015 reviews marine extremophiles and various uses of the specialized enzymes ("extremozymes") they make. Not surprisingly, there is considerable interest in the uses of extremophiles in human medicine. Babu, et al. 2015 provides a brief overview of these medical uses and demonstrates that the technological challenges of using extremophiles are being overcome to provide therapeutic uses directed at many medical problems.

An important applied use of extremophiles is to address pollution problems. As examples, Rivasseau, et al. 2013 (cited under Radiation) describes a green alga that can be used to decontaminate nuclear wastes, and Chaney, et al. 2014 summarizes the use of heavy-metal-tolerant plants to clean metal-polluted soils. As with other biological resources, exploiting extremophiles raises important ethical considerations about ownership and the distribution of profits derived from biotechnological or medical uses. These have been addressed by the Convention on Biodiversity, a global agreement signed by over 160 countries. Kamau, et al. 2015 is an excellent source of information on the Nagoya Protocol, a refinement of the Convention on Biodiversity aimed at clarifying issues pertaining to research and development using genetic resources, including those derived from organisms from extreme environments.

Anitori, Roberto Paul, ed. 2012. *Extremophiles: Microbiology and biotechnology*. Norfolk, UK: Caister Academic.

The eleven chapters in this edited book cover biotechnological applications of extremophiles (primarily prokaryotes). Uses of extremophiles that tolerate extreme temperature, pressure, salinity, ionizing radiation, and pH are highlighted.

Babu, Prasanti, Anuj K. Chandel, and Om V. Singh. 2015. *Extremophiles and their applications in medical processes*. SpringerBriefs in Microbiology. Cham, Switzerland: Springer.

This book is an excellent brief introduction to the medical uses of extremophiles. It covers extremophile survival mechanisms, uses of extremophiles in therapies, and challenges in using extremophiles in therapeutic applications.

Chaney, Rufus L., Roger D. Reeves, Ilya A. Baklanov, et al. 2014. Phytoremediation and phytomining: Using plants to remediate contaminated or mineralized environments. In *Plant ecology and evolution in harsh environments*. Edited by Nishanta Rajakaruna, Robert S. Boyd, and Tanner B. Harris, 365–391. Environmental Research Advances. Hauppauge, NY: Nova Science.

This review describes how plants tolerant of extreme soil conditions can be used to address environmental problems such as contaminated soils. It also addresses the use of such tolerant plants to extract elements from soils as a less environmentally damaging alternative to traditional mining techniques.

Dalmaso, Gabriel Zamith Leal, Davis Ferriera, and Alane Beatriz Vermelho. 2015. Marine extremophiles: A source of hydrolases for biotechnological applications. *Marine Drugs* 13.4: 1925–1965.

This review is an excellent source of information on extremophiles from marine habitats and the specialized “extremozymes” that they produce. These enzymes work under harsh environmental conditions and thus have important uses in a variety of industries.

Giddings, Lesley-Ann, and David J. Newman. 2015. *Bioactive compounds from marine extremophiles*. SpringerBriefs in Microbiology. Cham, Switzerland: Springer.

An overview of compounds that have biological activity isolated from marine extremophiles, the book demonstrates the vast molecular potential of marine extremophiles. Early-21st-century advances in culturing marine microbes are allowing discovery of many new molecules, some of which are undergoing development as novel drugs.

Kamau, Evanson Chege, Gerd Vinter, and Peter-Tobias Stoll, eds. 2015. *Research and development on genetic resources: Public domain approaches in implementing the Nagoya Protocol*. Routledge Research in International Environmental Law. New York: Routledge.

This twenty-chapter edited book provides up-to-date information on the national and international legal frameworks involving research and development using genetic resources. Its contents are relevant to all biological research of this type, including that involving organisms from extreme environments.

Singh, Om V., ed. 2013. *Extremophiles: Sustainable resources and biotechnological implications*. Hoboken, NJ: Wiley-Blackwell.

The sixteen chapters in this edited book cover a wide range of topics regarding applied uses of extremophile prokaryotes or their bioproducts, including the challenges of culturing them along with their use in bioenergy, textile finishing, recovery of metals, and many other uses.

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