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Geoecology

[Nishanta Rajakaruna](#), [Robert S. Boyd](#)

Introduction

Geology plays a fundamental role in shaping the biotic world around us. Geologic history (plate tectonics and orogenic or mountain-building activity), landforms (geomorphology), and lithology (parent material and substrate) influence ecological and evolutionary processes and contribute to both macro- and micro-scale patterns of biogeography. Geoecology is an interdisciplinary and multidisciplinary science that integrates the geosciences with the life sciences, focusing on the myriad influences of geological processes on historical and contemporary patterns of biogeography, including the causes and consequences of geodaphics on biota at all temporal and spatial scales. At the same time, geoecology examines the role biota play in a range of geodaphic processes, including in weathering and pedogenesis, thereby altering the chemical and physical composition of the Earth's surface and its patterns of biodiversity. Geobiology (geobotany and geozoology), biogeography, and biogeochemistry are important subfields within geoecology. Much of earth's biotic heterogeneity is a direct result of ecological heterogeneity stemming from geodaphic influences. Early naturalists often associated the occurrence of certain plant species with particular geologies, leading to biogeochemical prospecting for highly sought after minerals and metals. Recent advances in biogeochemical studies have led to phytomining, the use of plants to extract metals such as nickel and gold from metal-enriched soils. Plant evolutionary ecology also has its roots in geoecology, with pioneering experimental studies highlighting the influence of landforms and geodaphics on plant fitness and the evolutionary process, leading to the development of the concept of ecotypes—genetically distinct populations that are locally adapted to specific habitats characterized by distinct environmental conditions. Chemically imbalanced (i.e., nutrient poor or metal rich) geologic materials, such as serpentinites, contribute greatly to biodiversity, with high levels of plant endemism in regions overlying such geologies. Study of these endemic plants has contributed to ecological and evolutionary theory as well as basic and applied aspects of conservation and restoration sciences. Recent advances in geographic information science (GIS) and remote sensing, including light detection and ranging (LiDAR) and satellite imagery, combined with advanced computational techniques, have also provided means to closely monitor changes in patterns and processes of biota spread across geologic, topographic, and related ecological gradients. Such advances have

led to effective conservation planning and better management of threats to biota resulting from stressors associated with climate change.

General Overviews

Geocology is the study of the multifaceted relationships that exist between substrate and biota. Parent materials, climate, topography, and time determine the kind of substrate that becomes available for colonization by biota, and their habitation further influences the nature of the substrate upon which plants grow and animals and microbes dwell. Humans have long observed the special associations between organisms and their substrate, and such knowledge has served as the foundation of biogeoprospecting, the use of organisms as indicators of minerals and chemical elements found within geologic material. [Martin and Coughtrey 1982](#) and [Brooks 1983](#) (cited under [Flora](#)) are excellent resources for the early literature on this topic, particularly in Europe. [Huggett 1995](#) is an authoritative treatment of geocology, providing an extensive discussion on the roles that climate, geology, soils, altitude, topography, insularity, and disturbance play in generating and maintaining patterns of biotic diversity. [Knoll, et al. 2012](#) is also a good resource for a solid foundation on geobiological topics, including the role of nutrient cycles in biological processes and biota as geobiological agents, in addition to information on geobiological weathering, paleogeobiology, and technological advances in geobiological research. Much of the research on geocology has focused on microbe- and plant-substrate relations. [Konhauser 2006](#) is an excellent introduction to the geocology of microbes, while [Kruckeberg 2002](#) is a comprehensive treatment on the roles that geology, topography, and geologic history play in shaping plant communities. Some plant-geology interactions have received more attention than others, particularly on serpentinites, due to their hosting unique communities containing a high proportion of endemic and rare species. [Roberts and Proctor 1992](#) is an early but comprehensive treatment on the ecology of serpentinite-associated plants. [Alexander, et al. 2007](#) explores the substrate-biota relationships for the serpentinites of western North America, a region that has been the focus of geocological investigations since the mid-1900s. For recent treatments on the ecology and evolution of serpentinite habitats, see [Brady, et al. 2005](#) and [Harrison and Rajakaruna 2011](#) (both cited under [Evolutionary Aspects](#)). Unlike studies for plants and microbes, studies examining the role of lithology on animals are relatively scarce (but see citations under [Fauna](#)). Animal studies typically focus on how geologic history and landforms (and associated climatic conditions) influence animal ecology and evolution. [Barrett and Peles 1999](#) is a good introductory resource for such information, including how landscape patterns and processes impact small mammals and how they, in turn, influence landscape structure and composition.

- Alexander, Earl B., Robert G. Coleman, Todd Keeler-Wolf, and Susan P. Harrison. 2007. *Serpentine geocology of western North America: Geology, soils and vegetation*. New York: Oxford Univ. Press.

This book explores the ecology of serpentinite rock outcrops in western North America, focusing on soils and plants but including information on other organisms, including animals, fungi, and other microorganisms where feasible.

- Barrett, Gary W., and John D. Peles, eds. 1999. *Landscape ecology of small mammals*. New York: Springer.

The fifteen chapters discuss case studies, providing new insights into how landscape patterns and processes impact small mammals and how small mammals, in turn, influence landscape structure and composition.

- Huggett, Richard J. 1995. *Geoecology: An evolutionary approach*. New York: Routledge.

The nine chapters introduce the reader to the structure and function of geoecosystems, their components, and their environment. The roles that climate, soils, geology, altitude, topography, insularity, and disturbance play in shaping biotic communities are a central focus of this book.

- Knoll, Andrew H., Donald E. Canfield, and Kurt O. Konhauser, eds. 2012. *Fundamentals of geobiology*. Oxford: Wiley-Blackwell.

The book is a thorough introduction to the use of molecular tools and stable isotopes in geobiological research, and to geobiology and associated topics such as the role of carbon, nitrogen, and other nutrient cycles in biological processes; geochemical origins of life; paleogeobiology; microbes; plants; animals; and humans as geobiological agents.

- Konhauser, Kurt O. 2006. *Introduction to geomicrobiology*. Malden, MA: Blackwell Science.

The seven chapters provide a comprehensive review of the role microbes play in shaping Earth's physical environments. Topics include biomineralization, microbial weathering, microbial role in contaminant mobility, bioremediation and biorecovery, the function of microorganisms in mineral dissolution and oxidation, and Earth's early microbial life, among others.

- Kruckeberg, Arthur R. 2002. *Geology and plant life: The effects of landforms and rock types on plants*. Seattle: Univ. of Washington Press.

The book explores the roles landforms, lithology, and geologic histories play in generating and maintaining plant diversity. It reviews the rich history of geobotanical studies; discusses geodaphic influences on plant life, including in ecological and evolutionary processes; and provides an overview of human influences on the geology-plant interphase.

- Martin, Michael H., and Peter J. Coughtrey. 1982. *Biological monitoring of heavy metal pollution: Land and air*. Dordrecht, The Netherlands: Springer.

Although published in the 1980s, the eight chapters provide an excellent overview of the historic and current uses of plants and animals to detect heavy metals in both natural and

anthropogenic settings. The primary focus is on the use of plants as effective monitors of heavy metals in rocks, soils, and air.

- Roberts, Bruce A., and John Proctor, eds. 1992. *The ecology of areas with serpentinized rocks: A world view*. Geobotany 17. Dordrecht, The Netherlands: Kluwer Academic.

After a brief geological review, thirteen contributed chapters cover serpentinite ecology in areas within North America, Europe, Africa, Australia, and Asia. Coverage reflects the limited state of knowledge at the time, but the book is a good entry point into the pre-1990s serpentinite ecology literature.

Journals

Papers regarding geoecology can be found in a variety of journals because this multidisciplinary and interdisciplinary topic is pertinent to many academic fields, including biogeochemistry, geobiology, biogeography, landscape ecology, evolution, conservation, and restoration. Important journals that publish papers involving geoecology include [*Journal of Biogeography*](#), [*Global Ecology and Biogeography*](#), and [*Diversity and Distributions*](#). All three journals frequently publish papers dealing with the roles played by geology and soil conditions in spatial, ecological, and historical biogeography of organisms. [*Plant and Soil*](#) publishes papers on all aspects of soil-plant interactions, including those examining how soil conditions contribute to local, regional, and global plant distributions. [*Geobiology*](#) is an interdisciplinary journal focusing on the relationships between biology and Earth's physical and chemical environment, while [*Geomicrobiology Journal*](#) explores aspects of microbial transformation of geologic materials and the impact such alterations have had on Earth and its biota through time. [*Journal of Geographic Information System*](#) and [*International Journal of Geographical Information Science*](#) publish basic and applied research on computational methods, including geographic information science (GIS) and light detection and ranging (LiDAR), available for the study of biotic patterns in both natural and anthropogenic landscapes. Approaches to the study of geoecology are diverse and are carried out worldwide and, thus, papers associated with geoecological topics can be found in numerous international journals; we have listed a few important journals publishing original research and comprehensive reviews on geoecological topics.

- [*Diversity and Distributions*](#). 1993–.

The focus of this journal includes papers dealing with the application of biogeographical principles, theories, and analyses to problems concerning the conservation of biodiversity.

- [*Geobiology*](#). 2003–.

The journal publishes papers on the relationships between life and Earth's chemical and physical environments, especially papers that contain both geological and biological elements.

- [*Geomicrobiology Journal*](#). 1978–.

The journal publishes research and review articles on microbial transformations of materials composing Earth's crust, focusing on bacteria, yeasts, filamentous fungi, microalgae, protists, and related microorganisms as geomechanical or geochemical agents.

- [*Global Ecology and Biogeography*](#). 1991–.

The journal publishes studies exploring broad and consistent patterns in the ecological characteristics of organisms and ecosystems, particularly those addressing general ecological hypotheses, using data of broad geographic, taxonomic, or temporal scope.

- [*International Journal of Geographical Information Science*](#). 1987–.

The journal provides a venue for papers on approaches, methods, and research relating to GIS. Research on the design, implementation, and use of GIS for monitoring species, predicting patterns of species distributions, and decision making for effective conservation planning and urban design is regularly published here.

- [*Journal of Biogeography*](#). 1974–.

The journal publishes original research papers and reviews dealing with all aspects of spatial, ecological, and historical biogeography. The journal is the primary source for biogeographical studies carried out globally, using recent advances in geocological research.

- [*Journal of Geographic Information System*](#). 2009–.

The journal frequently publishes theoretical and applied research on the use of GIS, high performance computing, and remote sensing methods such as LiDAR in detecting and analyzing distributional patterns of biota, especially vegetation, in natural and anthropogenic habitats.

- [*Plant and Soil*](#).

This journal covers fundamental and applied aspects of plant-soil interactions, including how differences in soil conditions contribute to differences in plant distributions. Additional topics include plant-soil-microbe relations.

Geologic, Pedologic, and Biotic Influences and Interactions

Geologic and pedologic processes greatly influence the ecology and evolution of biota. Vicariant events including plate tectonics, orogenic activities, and oceanic island formations lead to disjunctions in biota, contributing to geographic isolation and subsequent speciation. Further, they influence both regional and global patterns of biodiversity. The complex relationships between organisms and their substrate also involve interactions that affect both the substrate and its ecology. [Wardle 2006](#) stresses the need for examining aboveground biotic drivers of soil biodiversity to better understand community and ecosystem ecology and relationships between

biodiversity and ecosystem functioning. For example, soil crust-forming microbes exert a strong influence on water infiltration, carbon sequestration, and nutrient cycling, influencing the distribution and abundance of microbes, plants, and animals. [Martínez, et al. 2006](#) explores the role of biological soil crusts, demonstrating that crust formation by mosses and lichens depends on cover of bare soil and litter, soil respiration, potassium content, and aggregate stability. The fundamental role played by soil- and rock-community microbes, including desert biological soil crusts, in biogeochemical processes is further discussed in [Pointing and Belnap 2012](#) (cited under [Physiology and Genetics](#)). Similarly, [Ginzburg, et al. 2008](#) examines how soil-nesting activities of harvester ants influence pedologic properties and soil microbial diversity. Such bioturbation, as discussed in [Wilkinson, et al. 2009](#), is fundamental to understanding processes of soil formation, niche formation, and ecosystem evolution. The importance of edaphic features in maintaining regional soil biodiversity is further stressed in [Birkhofer, et al. 2012](#). The authors conclude that soil properties explain significant proportions of variation in fungal and soil fauna abundance and diversity, even after accounting for heterogeneity resulting from large-scale differences among sampling locations and land-use types. Similar influences of geodaphic factors are noted in aboveground patterns of biodiversity. [Higgins, et al. 2011](#) demonstrates how geologic and edaphic features control floristic diversity within Amazonian forests, and that proper management requires a regional approach that takes geodaphic-biotic affinities into consideration. [Zhang, et al. 2013](#) examines the relative importance of topography and edaphic properties in the assembly of karst-adapted plant communities. The authors' work suggests that steepness of slope and depth of soil are critical factors in the formation of plant communities within karst forests. Further, historic geological events such as tectonics and orogenic activity greatly influence biogeography, ecology, and evolution. [Wright and Stigall 2013](#) uses phylogenetic biogeographic analyses to examine how historic geologic and oceanographic processes have influenced brachiopod speciation and patterns of dispersal. Additional references for biogeographic patterns that have resulted from vicariant events are cited under [Biogeography](#).

- Birkhofer, Klaus, Ingo Schöning, Fabian Alt, et al. 2012. General relationships between abiotic soil properties and soil biota across spatial scales and different land-use types. *PLoS ONE* 7.8: e43292.

The paper explores the relationships between soil properties and soil biota across large spatial scales and different land-use types spanning the latitudinal gradient of Germany. Abiotic soil properties explained significant amounts of variation in fungal, meso- and macrofauna, but not in yeast or bacterial biomass or diversity.

- Ginzburg, Orit, Walter G. Whitford, and Yosef Steinberger. 2008. Effects of harvester ant (*Messor* spp.) activity on soil properties and microbial communities in a Negev desert ecosystem. *Biology and Fertility of Soils* 45:165–173.

The study reports changes in soil microbial biomass and functional diversity resulting from harvester ant activity. Ant activity increased organic matter, soluble nitrogen, and microbial activity in nest-modified soils in comparison to control soils, suggesting that the effect of nests on soil fertility results from increased microbial biomass and activity.

- Higgins, Mark A., Kalle Ruokolainen, Hanna Tuomisto, et al. 2011. Geological control of floristic composition in Amazonian forests. *Journal of Biogeography* 38:2136–2149.

The study reports that Amazonian forests are partitioned into large-area units based on geologic and edaphic features, and the evolution of the units through geological time provides a mechanism for species diversification. Thus, it concludes that land use, management, and conservation approaches must be implemented on a regional basis.

- Martínez, Isabel, Adrián Escudero, Fernando T. Maestre, Azucena de la Cruz, César Guerrero, and Augustin Rubio. 2006. Small-scale patterns of abundance of mosses and lichens forming biological soil crusts in two semi-arid gypsum environments. *Australian Journal of Botany* 54:339–348.

The authors test whether the spatial patterning of lichens and mosses is related to surface and subsurface soil variables in two semiarid gypsum environments in Spain. Their results show that bare soil and litter cover, soil respiration, potassium content, and aggregate stability are drivers of biological soil crust composition and abundance.

- Wardle, David A. 2006. The influence of biotic interactions on soil biodiversity. *Ecology Letters* 9:870–886.

This review examines the biotic factors and mechanisms influencing soil community diversity across spatial scales. It concludes that a better understanding of biotic drivers of soil biodiversity are important to address topics in community and ecosystem ecology, such as aboveground-belowground interactions and the relationship between biodiversity and ecosystem functioning.

- Wilkinson, Marshall T., Paul J. Richards, and Geoff S. Humphreys. 2009. Breaking ground: Pedological, geological, and ecological implications of soil bioturbation. *Earth-Science Reviews* 97:257–272.

Bioturbation, resulting from the stirring and mixing of soil and sediments by organisms, is discussed as a fundamental process contributing to soil and landscape evolution, ecosystem engineering, niche construction, and carbon cycling.

- Wright, David F., and Alycia L. Stigall. 2013. Geologic drivers of late Ordovician faunal change in Laurentia: Investigating links between tectonics, speciation, and biotic invasions. *PLoS ONE* 8.7: e68353.

The paper investigates causal links between a dramatic turnover in orthid brachiopods and two dominant geologic processes, the Taconian Orogeny and Guttenberg carbon isotope excursion (GICE)-related global cooling, operating within Laurentia during the late Ordovician. Phylogenetic biogeographic analyses reveal how geologic and oceanographic processes have influenced brachiopod speciation and patterns of dispersal.

- Zhang, Zhong-hua, Gang Hu, and Jian Ni. 2013. Effects of topographical and edaphic factors on the distribution of plant communities in two subtropical karst forests, southwestern China. *Journal of Mountain Science* 10:95–104.

Study of relationships between topography and edaphic properties and the distribution of plant communities suggests that topographical factors are more important than edaphic factors in influencing local plant distribution on steep slopes with extensive rock outcrops, while edaphic factors are more influential on gentle slopes and relatively deep soils.

Biological Weathering

Mineral weathering of rocks and soils is an important process of nutrient element release in forms available for plant and microbial uptake. Mineral weathering is a pedological process responsible for the development of soils upon or within which many organisms live and, therefore, a fundamental aspect of geocology. Changes in the mode and rate of weathering can influence the type of soil that is produced and the ecology of the habitats overlying those soils. Organisms such as bacteria, fungi, lichens, plants, invertebrates, and other animals play a critical role in the weathering of rocks and soils, including in modifying the soil structure that impacts infiltration, drainage, aeration, pH, cation exchange capacity, and nutrient availability. Thus, any variation in biological weathering of minerals and the formation of soils can have a direct effect on ecology in both below- and aboveground habitats, and therefore can affect biodiversity. [Abbott and Murphy 2007](#) is a good resource for an overview of the role fauna, flora, and microbes play in the chemical and physical weathering of minerals and the formation of soils. Plants play an important role in weathering via the mechanical/physical actions of their roots and by the chemicals they secrete into the rhizosphere for facilitating or restricting ion uptake, or for defensive (or allelopathic) purposes. [Lucas 2001](#) and [Andrews, et al. 2008](#) are two good sources to explore aspects of weathering and soil formation under the influence of plants. Microbial weathering has attracted much attention over the last several decades. [Uroz, et al. 2009](#) is a useful source for information on bacterial weathering, while [Hoffland, et al. 2004](#) explores the role of fungi in mineral weathering and pedogenesis. Plant-fungal-mineral interactions are the focus of a study, [Smits, et al. 2008](#), that shows the intricate and reciprocal relationships that ectomycorrhizal fungi have with plants (enabling them to be effective agents of mineral weathering). Lichen influences on mineral weathering have also been a focus of investigations in recent decades. [Chen, et al. 2000](#) is an early but comprehensive review of the processes of chemical and physical weathering of rocks by lichens. The study of biological weathering, especially by bacteria and fungi, also has wide-ranging applications in biotechnology. [Mapelli, et al. 2012](#) is an excellent source for a discussion on how findings from microbe-substrate weathering studies can contribute to the fields of agriculture, bioremediation, and other bioremediation and environmental technologies.

- Abbott, Lynette K., and Daniel V. Murphy, eds. 2007. *Soil biological fertility: A key to sustainable land use in agriculture*. Dordrecht, The Netherlands: Springer.

The volume consists of twelve chapters on biological aspects of soil fertility, including the role animals, plants, fungi, and other microorganisms play in the chemical and

physical transformation of soil. While the focus is on soil fertility for agricultural purposes, the information is pertinent to other topics in geoecology.

- Andrews, Megan Y., Jay J. Ague, and Robert A. Berner. 2008. Weathering of soil minerals by angiosperm and gymnosperm trees. *Mineralogical Magazine* 72:11–14.

The paper examines quantitative weathering rates of angiosperms and gymnosperms by investigating their plant-mineral interactions in a temperate field setting underlain by granodiorite. The observed root-mineral interactions suggest slightly more weathering of Ca-bearing minerals by the angiosperms, and significantly more weathering of the Mg-bearing minerals by the gymnosperms.

- Chen, Jie, Hans-Peter Blume, and Lothar Beyer. 2000. Weathering of rocks induced by lichen colonization: A review. *Catena* 39:121–146.

The review discusses the role lichens play in the weathering of rock and other mineral substrates. Physically induced weathering—caused by mechanical disruption of rocks by hyphal penetration and expansion, and by contraction of lichen thalli and chemically induced weathering via the excretion of various organic acids (particularly oxalic acid)—is highlighted.

- Hoffland, Ellis, Thomas W. Kuyper, Håkan Wallander, et al. 2004. The role of fungi in weathering. *Frontiers in Ecology and the Environment* 2:258–264.

The review is an excellent source of information on the taxonomy and ecology of fungi responsible for biological weathering and the physical and chemical means by which fungi weather rocks. Areas of future research on fungal-mineral interactions are also highlighted.

- Lucas, Yves. 2001. The role of plants in controlling rates and products of weathering: Importance of biological pumping. *Annual Review of Earth and Planetary Sciences* 29:135–163.

The critical role plants play in controlling the rates and products of weathering is the topic of this review. The influences of plants in controlling water dynamics, mechanical weathering, and the chemistry of weathering solutions are highlighted.

- Mapelli, Francesca, Ramona Marasco, Annalisa Balloi, et al. 2012. Mineral–microbe interactions: Biotechnological potential of bioweathering. *Journal of Biotechnology* 157:473–481.

The roles of bacteria and fungi in mineral dissolution are discussed in relation to their biotechnological potential, including in increasing crop productivity in arid lands, bioremediation, and other bioremediation and environmental technologies.

- Smits, Mark M., Steeve Bonneville, Simon Haward, and Jonathan R. Leake. 2008. Ectomycorrhizal weathering, a matter of scale? *Mineralogical Magazine* 72:131–134.

The paper investigates plant-fungal-mineral interactions, showing that ectomycorrhizal fungi are actively engaged in the weathering of apatite and biotite, and that carbon from a tree is actively transported to the fungus where it is preferentially allocated to areas with minerals containing weatherable supplies of essential nutrients.

- Uroz, Stéphane, Christophe Calvaruso, Marie-Pierre Turpault, and Pascale Frey-Klett. 2009. Mineral weathering by bacteria: Ecology, actors and mechanisms. *Trends in Microbiology* 17:378–387.

The paper discusses the ecological relevance of bacterial weathering and highlights molecular mechanisms and genetic determinants involved in the dissolution of complex minerals under aerobic conditions, and potential applications of genomic resources to the study of bacterial weathering.

Extremophiles

Extremophiles are organisms able to thrive under conditions inhospitable for most other biota. While there is much attention on microbes as model organisms for the study of extremophile ecology, physiology, genetics, and evolution, the study of plants and animals of extreme geodaphic settings, such as alkaline, acidic, hypersaline, and metal-enriched substrates, has also generated much interest in recent years. [Bell 2012](#) and [Rampelotto 2013](#) are comprehensive treatments containing original research and review papers on plants, animals, and microbes found in extreme settings, including those that have arisen from geologic or edaphic phenomena. Plant-specific literature deals with adaptations to chemically extreme substrates such as serpentinites as illustrated in [Brady, et al. 2005](#) (cited under [Evolutionary Aspects](#)), and to gypsum and dolomite as discussed in [Escudero, et al. 2014](#) and [Pignatti and Pignatti 2014](#) (cited under [Flora](#)), respectively. [Jenks and Hasegawa 2014](#) (cited under [Physiology and Genetics](#)) reports on early-21st-century discoveries of adaptations to common geodaphic stresses encountered by plants, including salinity, heavy metals, drought, and flooding. There is extensive literature summarizing microbial extremophiles in terrestrial and aquatic landscapes. [Seckbach 2007](#) (cited under [Bacteria, Protists, Fungi, and Lichens](#)) is an excellent source for information on the diversity, ecology, and physiology of algae and cyanobacteria tolerant of extreme environments. [Margesin and Miteva 2011](#) reviews microbe adaptations to cold environments, while [Cardace and Hoehler 2011](#); [McCollom and Seewald 2013](#); and [Takai, et al. 2005](#) discuss microbial evolution in, and tolerance to, serpentinite habitats. As the serpentinization process creates highly reducing conditions, producing hydrogen and methane for metabolic energy, serpentinites are a prime target for the study of early life. [Pikuta, et al. 2007](#), while providing a good general overview of microbial tolerances to various extreme environments, highlights advances in the study of microfossils in meteorites and the significance of microbial extremophiles to the study of astrobiology. [Gerday and Glansdorff 2007](#) provides a comprehensive review of the biochemical and physiological bases for tolerance among thermophiles, psychrophiles, halophiles, acidophiles, piezophiles, and alkaliphiles, and discusses biotechnological applications of extremophiles.

- Bell, Elanor. 2012. *Life at extremes: Environments, organisms, and strategies for survival*. Oxford: CABI.

This authoritative treatment describes the biological, ecological, and biogeochemical challenges faced by microbes, plants, and animals living in harsh environments worldwide, including polar environments and hot deserts; acidic, alkaline, and hypersaline flats; caves and karst settings; and terrestrial and deep sea hydrothermal vents.

- Cardace, Dawn, and Tori M. Hoehler. 2011. Microbes in extreme environments: Implications for life on the early Earth and other planets. In *Serpentine: The evolution and ecology of a model system*. Edited by Susan P. Harrison and Nishanta Rajakaruna, 29–48. Berkeley: Univ. of California Press.

This chapter discusses how serpentinizing systems serve as habitat for extremophile microbes (those inhabiting the high-pH, Ca²⁺-rich waters circulating in serpentinite bodies) and how they provide novel ground for scientific investigation into extremophile evolution and life on other planets.

- Gerday, Charles, and Nicolas Glansdorff, eds. 2007. *Physiology and biochemistry of extremophiles*. Washington, DC: ASM.

The book provides a comprehensive review of the physiological ecology, biochemistry, evolutionary aspects, and biotechnological applications of all known types of extremophiles, including thermophiles, psychrophiles, halophiles, acidophiles, piezophiles, and alkaliphiles.

- Margesin, Rosa, and Vanya Miteva. 2011. Diversity and ecology of psychrophilic microorganisms. *Research in Microbiology* 162:346–361.

The review focuses on the abundance, taxonomic, and functional biodiversity; low temperature adaptation; and biogeography of microbial communities belonging to *Bacteria*, *Archaea*, and *Eukarya* from a range of aquatic and terrestrial cold environments.

- McCollom, Thomas M., and Jeffrey S. Seewald. 2013. Serpentinites, hydrogen, and life. *Elements* 9.2: 129–134.

The paper describes how serpentinization creates highly reducing conditions, producing hydrogen and methane that can then be used by some microorganisms for generating metabolic energy and biomass, making serpentinites a major focus in the study of the origin of life on Earth and elsewhere in our solar system.

- Pikuta, Elena V., Richard B. Hoover, and Jane Tang. 2007. Microbial extremophiles at the limits of life. *Critical Reviews in Microbiology* 33:183–209.

The review discusses the status to date in all fields of extremophiles and summarizes the limits of life for different species of microbial extremophiles. Early-21st-century studies of microfossils in meteorites are also highlighted to discuss the significance of microbial extremophiles to astrobiology.

- Rampelotto, Pabulo H., ed. 2013. *Special issue: Extremophiles and extreme environments*. *Life* 3:1–517.

The volume devotes three issues to the discussion of wide-ranging topics relating to microbial and other extremophiles inhabiting terrestrial and aquatic habitats. The papers in this volume focus on extremophile diversity, ecology, physiology, genetics, and evolution. Available [online](#).

- Takai, Ken, Craig L. Moyer, Masayuki Miyazaki, et al. 2005. *Marinobacter alkaliphilus* sp. nov., a novel alkaliphilic bacterium isolated from seafloor alkaline serpentine mud from Ocean Drilling Program Site 1200 at South Chamorro Seamount, Mariana Forearc. *Extremophiles* 9.1: 17–27.

Physiological and molecular approaches are used to identify a new bacterium species isolated from a sub-seafloor serpentinite mud volcano, illustrating the potential of serpentinite sites to harbor undescribed species.

Bacteria, Protists, Fungi, and Lichens

Terricolous (soil dwelling) and saxicolous (rock dwelling) microorganisms and lichens play a fundamental role in the ecology of both below- and aboveground habitats via their influence on biogeochemical processes, including weathering, pedogenesis, nutrient cycling, and nutrient acquisition by plants. Thus, much attention has been paid to characterize the biodiversity of such organisms, including the important role they play in biogeochemical processes. [Kirchman 2012](#) is an excellent resource for information on microbial geocology and biogeochemistry.

Microorganisms and lichens associated with unusual and often-extreme geodaphic settings have been a focus of many investigations, primarily due to their unique physiological and biochemical adaptations to their chemically and physically harsh substrate. [Beyer and Bölter 2002](#) examines the ecology of microbes and other biota found in ice-free Antarctic landscapes. The chapter on heterotrophic microbes and their microbial and enzymatic activities is especially relevant to microbial geocology. Ultramafic (iron- and magnesium-rich) rocks have also been a focus of geocological study (see [Brady, et al. 2005](#) and [Harrison and Rajakaruna 2011](#), both cited under [Evolutionary Aspects](#)) due to the unusual soils they generate and the unique biota they harbor. [Southworth, et al. 2014](#) reviews ectomycorrhizal and arbuscular mycorrhizal symbioses on and off ultramafic soils. [Rajakaruna, et al. 2012](#) examines lichens of ultramafic and nonultramafic rocks in California and concludes that the lichens often differ between rock types, and that species richness is greater on ultramafic rocks. The authors suggest that a combination of chemical and physical attributes of the rocks may drive the diversity of saxicolous lichens. The microbial ecology of heavy metal-rich soils is also a major focus due to its biotechnological and bioremediation potential. [Giller, et al. 2009](#) is a good resource on this topic. Salinity is another stressor impacting soils worldwide. [Casamayor, et al. 2013](#) demonstrates the use of modern

genetic tools to characterize microbial diversity of saline lakes. The role that land-use history can play in bacterial diversity is the focus of the study in [Guan, et al. 2013](#). The authors conclude that the bacterial communities are influenced by both geochemical factors and land-use practices, and that agricultural lands harbor more homogenized communities compared to those in pristine settings. While aspects of bacterial and fungal geocology have received much attention, the literature on protists and other eukaryotic microbes is limited. [Seckbach 2007](#), however, is a good resource for studies on the diversity, ecology, and physiology of stress-tolerant algae and cyanobacteria. [Bell 2012](#) and [Rampelotto 2013](#) (both cited under [Extremophiles](#)) also contain useful information regarding the diversity and geocology of microbes.

- Beyer, Lothar, and Manfred Bölder, eds. 2002. *Geocology of Antarctic ice-free coastal landscapes*. Ecological Studies 154. Berlin: Springer.

This volume describes typical terrestrial environments of the maritime and continental Antarctic, focusing on interactions among soils, microbes, plants, and animals. One chapter is devoted to the discussion of heterotrophic microbes and their microbial and enzymatic activities in Antarctic soils.

- Casamayor, Emilio O., Xavier Triadó-Margarit, and Carmen Castañeda. 2013. Microbial biodiversity in saline shallow lakes of the Monegros Desert, Spain. *FEMS Microbiology Ecology* 85:503–518.

The paper reports the findings from a rRNA gene fingerprinting and sequencing study of the diversity of bacteria, archaea, and microbial eukaryotes from saline lakes with large salinity (2.7–22.1 percent) and temperature ranges (1.5–35.3°C). The groups exhibited differential tolerances to the abiotic stresses and often dominated distinct habitats.

- Giller, Ken E., Ernst Witter, and Steve P. McGrath. 2009. Heavy metals and soil microbes. *Soil Biology and Biochemistry* 41:2031–2037.

Advances in the ecotoxicological assessment of heavy metals and their effects on soil organisms are the focus of this review. The need for long-term experiments and basic research on how microorganisms are exposed to and respond to metals in soils is also emphasized.

- Guan, Xiangyu, Jinfeng Wang, Hui Zhao, et al. 2013. Soil bacterial communities shaped by geochemical factors and land use in a less-explored area, Tibetan Plateau. *BMC Genomics* 14:820–833.

The study shows that the bacterial community structure and functions are influenced by both human activities and soil environmental properties, and that the bacterial communities appeared to be more homogenized in farmland soils compared to pristine alpine meadows. Available [online](#).

- Kirchman, David L. 2012. *Processes in microbial ecology*. New York: Oxford Univ. Press.

The fourteen chapters are an excellent introduction to the ecology of viruses, bacteria, fungi, protozoa, and other protists in freshwater, marine, and terrestrial ecosystems. The primary focus of the book is microbial influences on biogeochemical processes.

- Rajakaruna, Nishanta, Kerry Knudsen, Alan M. Fryday, et al. 2012. Investigation of the importance of rock chemistry for saxicolous lichen communities of the New Idria serpentinite mass, San Benito County, California, USA. *Lichenologist* 44.5: 695–714.

This is one of only a handful of comparative studies of lichens of serpentinite and nonserpentinite rocks in North America. Lichen assemblages between the two rock types were significantly different at the species level but not at the generic level, with species richness significantly greater on the serpentinite rocks.

- Seckbach, Joseph, ed. 2007. *Algae and cyanobacteria in extreme environments*. Cellular Origin, Life in Extreme Habitats and Astrobiology 11. Dordrecht, The Netherlands: Springer.

The edited volume provides an overview of protists that dominate extreme environments, including those resulting from geodaphic processes. The diversity, ecology, physiology, and evolution of species found under extreme levels of temperature, pH, salt concentrations, UV radiation, moisture, heavy metals, anaerobic conditions, illumination, and hydrostatic pressure are discussed.

- Southworth, Darlene, Linda E. Tackaberry, and Hugues B. Massicotte. 2014. Mycorrhizal ecology on serpentine soils. *Plant Ecology and Diversity* 7.3: 445–455.

This review asks whether the diversity of plants on serpentinite-derived soils correlates with that of mycorrhizal fungi. Plants formed abundant ectomycorrhizal and arbuscular mycorrhizal symbioses both on and off of serpentinite. Ectomycorrhizal fungal communities did not differ between soil types, but arbuscular mycorrhizal communities differed in some cases and not others.

Flora

The geocology of plants has been a primary focus of studies in natural history, biogeochemistry, ecology, evolution, conservation biology, and the agricultural sciences. The intimate and inseparable relationship between plants and their substrate results from the need for plants to obtain water and nutrients from the substrate upon which they grow. Thus, it is no surprise that chemical and physical attributes of the substrate control many aspects of plant ecology and evolution. Throughout history, plants closely associated with specific geologies have been described as indicators of minerals and elements found within them, and close observation of such substrate-plant relations has led to biogeochemical prospecting worldwide. [Brooks 1983](#) and [Martin and Coughtrey 1982](#) (cited under [General Overviews](#)) are excellent resources for the early literature on plants adapted to heavy metal and other mineral-rich geologies. Current geocological treatments are primarily involved in describing unique floras associated with chemically and physically harsh geodaphic conditions. In this regard, much attention has been

paid to endemic- and rare plant-rich communities of serpentinite rocks. [Brooks 1987](#) and [Roberts and Proctor 1992](#) (cited under [General Overviews](#)) are excellent early resources for serpentinite-associated floras. More recent treatments include [Kruckeberg 2002](#) and [Alexander, et al. 2007](#) (both cited under [General Overviews](#)), along with [Brady, et al. 2005](#) and [Harrison and Rajakaruna 2011](#) (both cited under [Evolutionary Aspects](#)). Calcium-rich, alkaline geodaphic settings also contribute to distinct floras with high percentages of rare and endemic species. [Escudero, et al. 2014](#) is an up-to-date treatment on gypsum- (calcium sulfate) adapted plants, while [Pignatti and Pignatti 2014](#) covers dolomite- (calcium magnesium carbonate) associated floras of Europe. Plants associated with unique geomorphological features (mountains, deserts, peatlands, etc.) have also been of interest due to the unique adaptations they possess to tolerate climatic and other abiotic and biotic stressors. [Körner 2003](#) is a comprehensive treatment of the physiological ecology and evolution of plants in alpine environments. [Ward 2009](#) is an outstanding resource for plant adaptations to desert environments, while [Rydin and Jeglum 2006](#) is an authoritative treatment of plants in peatlands. The latter three references also deal with climate change-associated stressors influencing these unique plant communities, providing insight on how best to approach their management, conservation, and restoration. [Anderson, et al. 1999](#), although a little outdated, is a broad overview of the floristics, ecology, and conservation of specialized plant communities of edaphic islands and other unusual geocological settings in North America.

- Anderson, Roger C., James S. Fralish, and Jerry M. Baskin, eds. 1999. *Savannas, barrens, and rock outcrop plant communities of North America*. Cambridge, UK: Cambridge Univ. Press.

The twenty-six chapters discuss climate, geology, soils, and historic and current vegetation of plant communities of savannas, woodlands, barrens, and rock outcrops throughout the United States and Canada. The book provides an excellent overview of North America's edaphic islands and their unique vegetation, including their conservation, restoration, and management.

- Brooks, Robert R. 1983. *Biological methods of prospecting for minerals*. New York: John Wiley.

A useful resource listing plant and animal species associated with metal-enriched geologies worldwide. Chapter discussions include the history of geobotany in mineral exploration, plant communities used as indicators of mineralization, and plant species effective for indicating a range of widespread heavy metals.

- Brooks, Robert R. 1987. *Serpentine and its vegetation: A multidisciplinary approach*. Ecology, Phytogeography and Physiology 1. Portland, OR: Dioscorides.

An early overview of serpentine geocology, this volume provides a summary of research on serpentinite habitats worldwide, including information on soils, plants, animals, and agriculture.

- Escudero, Adrián, Sara Palacio, Fernando Maestre, and Arantzazu Luzuriaga. 2014. Plant life on gypsum: A review of its multiple facets. *Biological Reviews*.

All aspects of plant life on gypsum, from species to ecosystem levels, are discussed along with the processes related to the structure of gypsum plant communities. Research on the ecology and evolution of gypsum plants is highlighted and putative mechanisms to tolerate and adapt to gypsum soils are summarized.

- Körner, Christian. 2003. *Alpine plant life: Functional plant ecology of high mountain ecosystems*. 2d ed. Heidelberg, Germany: Springer.

The book covers a wide range of topics of alpine environments worldwide, including climate and substrate, floristics and phytogeography, physiological ecology, and anthropogenic impacts on alpine vegetation.

- Pignatti, Erika, and Sandro Pignatti. 2014. *Plant life of the dolomites: Vegetation structure and ecology*. New York: Springer.

Using the authors' extensive combined research, the book explores biological, geological, climatic, and physiochemical parameters of dolomite-associated plant communities in Europe, including their floristic composition, indicator taxa, habitat alteration risks, and conservation value.

- Rydin, Hakan, and John K. Jeglum. 2006. *The biology of peatlands*. New York: Oxford Univ. Press.

The book provides an overview of the ecology of peatlands (marsh, swamp, fen, and bog) and the adaptations of plants and other biota to moss-dominated permanent wetlands. Management, conservation, and restoration of peatlands are also discussed along with the influences of climate change on their biota.

- Ward, David. 2009. *The biology of deserts*. New York: Oxford Univ. Press.

The eleven chapters in this comprehensive treatment on the biology, ecology, and evolution of desert plants and animals covers wide-ranging topics associated with this arid and resource-poor ecosystem, including stressors impacting desert plants worldwide. It also emphasizes applied issues such as desertification and invasive species, and desert conservation.

Fauna

Since plants are a major component of the habitat of animals, geology often affects faunas indirectly through its effects on vegetation or climate. Direct effects are more subtle, but occur in many ways. Some geological substrates, such as limestone, are especially prone to the formation of caves, and these subterranean habitats have fascinating specialized and unique faunas: [Lin and Li 2014](#) (cited under [Conservation](#)) describes five new spider species from caves in China.

[Culver and Pipan 2009](#) provides an excellent general overview of cave environments and the biological processes that generate and sustain their biota. Some geological materials produce substrates with colors (black, white, red, etc.) that are important habitat components for animals. Substrate color affects soil temperature: [Hadley, et al. 1992](#) illustrates how black volcanic sand versus white sand beaches influences the ecology and behavior of tiger beetles in New Zealand. Substrate color also influences the visibility of animals to predators, and there are many examples of animal color evolving to match that of the substrate. [Linnen, et al. 2013](#) provides an example by investigating the evolution of the light coat color in deer mice from light-colored soils in the Nebraska Sandhills, United States. Another habitat feature influenced by geology is soil texture: this can directly influence the ability of animals to burrow or affect the structural integrity of burrows. [M'Rabet, et al. 2007](#) describes the importance of soil texture to burrow construction of an endangered spider. It also should be recognized that animals can affect landscapes, and the importance and extent of their effects can differ depending on geology. [Butler 1995](#) provides a good overview of animal impacts on landscapes and the associated literature prior to that date. The fauna of island habitats (both oceanic and edaphic) has received much study (see section on [Biogeography](#)): Foster's Rule, which contends that many island faunas evolve smaller (dwarfism) or larger (gigantism) sizes than mainland animals, is a fascinating example. [Case 1978](#) is a classic paper that helped establish Foster's Rule and stimulate its continuing investigation by biogeographers in the early 21st century. Other island biogeography concepts are often applicable to faunas restricted to unique geological areas. As an example, [Michael, et al. 2008](#) studied the reptile fauna of granite outcrops in southeastern Australia, finding that many factors (patch size, matrix condition, habitat structure, etc.) affected reptile diversity.

- Butler, David R. 1995. *Zoogeomorphology: Animals as geomorphic agents*. New York: Cambridge Univ. Press.

Good overview of how animal activities (burrowing, trampling, soil ingestion, etc.) change landscape features (by erosion and transport/deposition of sediment) and thus are a powerful ecological force. Terrestrial animals (including invertebrates) are emphasized, but aquatic animals are also included.

- Case, Ted. 1978. A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* 59:1–18.

The author expands on Foster's initial work to explore both island gigantism and dwarfism, setting the theoretical stage for later biogeographers. Foster's Rule continues to stimulate research, and its tenets are debated in the ecological and evolutionary literature.

- Culver, David, and Tanja Pipan. 2009. *The biology of caves and other subterranean habitats*. New York: Oxford Univ. Press.

A good introduction to the fauna of caves and related scientific literature. The book focuses on important biological topics including adaptation, speciation, community ecology, and conservation of cave biota.

- Hadley, Neil F., Anthony Savill, and Thomas D. Schulz. 1992. Coloration and its thermal consequences in the New Zealand tiger beetle *Neocicindela perhispidata*. *Journal of Thermal Biology* 17:55–61.

This paper is an excellent example of how substrate color (beaches made of either black or white sand) influences its temperature and how the behavior of an insect species occupying these habitats is modified in response.

- Linnen, Catherine, Yu-Ping Poh, Brant Peterson, et al. 2013. Adaptive evolution of multiple traits through multiple mutations at a single gene. *Science* 339:1312–1316.

Finding greater predation risk for mice whose coat color does not match soil color, the authors explore the origins of light coat color found in mice on sandy soils. They discovered that multiple mutations in a single gene have independently resulted in the adaptive light coloration of these mice.

- Michael, Damlan, Ross Cunningham, and David Lindenmayer. 2008. A forgotten habitat? Granite inselbergs conserve reptile diversity in fragmented agricultural landscapes. *Journal of Applied Ecology* 45:1742–1752.

Applying island biogeography concepts to granite outcrops, the authors generally find results congruent with theory. They conclude that reptile conservation is maximized when features of both the outcrop and the surrounding habitat matrix can be manipulated to favor reptile persistence.

- M'Rabet, Salima Machkour, Yann Hénaut, Alejandra Sepúlveda, Roberto Rojo, Sophie Calmé, and Violette Geissen. 2007. Soil preference and burrow structure of an endangered tarantula, *Brachypelma vagans* (Mygalomorphae: Theraphosidae). *Journal of Natural History* 41:1025–1033.

This study revealed that soil features were important to burrow construction, and that clay soils were preferred over sandy soils or soils with large amounts of roots. This information can help managers interested in conserving this rare species in remaining populations or reintroducing it at other sites.

Biogeography

Geology is one of many factors that influence the distribution of organisms across Earth's surface. Organisms are usually distributed in a patchy manner, and geology is an important habitat feature that often contributes to patchiness. [Cox and Moore 2010](#) provides an excellent overview of the general field of biogeography, including both classic and more recent literature. Patchy habitats can be terrestrial islands in an aquatic matrix (e.g., oceanic islands), and classical Island Biogeography Theory was first developed for these situations. [Whittaker and Fernández-Palacios 2007](#) is a good introduction to island biogeography, including the history of the field. [Bramwell and Caujape-Castells 2011](#) provides an exploration of the biology and ecology of island floras, including ecological and evolutionary perspectives as well as important

conservation implications. Islands can also be edaphic, when geological differences give rise to habitats that form patches within a matrix of very different soils. There has been much interest in applying Island Biogeography Theory to these edaphic islands, and in general the theory's predictions have been found to hold. [Schenk 2013](#) tests the prediction that dispersal ability in the plant genus *Mentzelia* should evolve to limit dispersal in species endemic to patches of gypsum soils. As theory predicts, the researcher finds that seeds of edaphic endemics of this wind-dispersed plant genus have smaller wings and thus have restricted dispersal abilities. Edaphic factors are an important contributor to plant speciation (see section on [Evolutionary Aspects](#)). [Fine, et al. 2013](#) explores edaphic specialist and generalist tree species in the most species-rich habitat on Earth, lowland tropical rainforest, concluding that edaphic variability is an important factor promoting genetic differentiation in tropical tree species. The importance of soil diversity to biological diversity is recognized by the concept of soil endemism. The exploration in [Bockheim and Schliemann 2014](#) of the contribution of soil endemism to plant endemism in Wisconsin, United States, showed a weak correlation. High mountains also contribute to unique patterns of biodiversity, and [Nagy and Grabherr 2009](#) and [Körner 2003](#) (cited under [Flora](#)) provide excellent overviews of the biogeography of alpine environments. Finally, there are important applications of biogeography for conservation. [Ladle and Whittaker 2011](#) provides a good introduction to these applications, which are further explored in the section on [Conservation](#).

- Bockheim, James G., and Sarah A. Schliemann. 2014. Soil richness and endemism across an environmental transition zone in Wisconsin, USA. *Catena* 113:86–94.

Testing the concept that soil endemism should be positively correlated with plant endemism, the authors examine soil and plant distributions across a transition zone. They find that plant endemism correlated more closely with landform than to soil taxa, but still report important associations between geological substrate and plant species distributions.

- Bramwell, David, and Juli Caujape-Castells. 2011. *The biology of island floras*. Cambridge, UK: Cambridge Univ. Press.

This edited volume contains twenty-one chapters covering a wide range of topics focused on island plant communities. Some chapters focus on specific islands, whereas others deal more broadly with topics such as reproductive biology, ecology, invasive species, conservation, climate change, etc.

- Cox, C. Barry, and Peter D. Moore. 2010. *Biogeography: An ecological and evolutionary approach*. 8th ed. Hoboken, NJ: John Wiley.

A broad overview of the field of biogeography, this book is a good introduction to the principles of the field and its underlying literature.

- Fine, Paul, Felipe Zapata, Douglas Daly, et al. 2013. The importance of environmental heterogeneity and spatial distance in generating phylogenetic structure in edaphic specialist and generalist tree species of *Protium* (Burseraceae) across the Amazon basin. *Journal of Biogeography* 40:646–661.

The authors build on prior work done in this rainforest system that contains edaphic specialist and generalist species. After examining the genetic structuring of two species, they conclude that edaphic heterogeneity is an important mechanism promoting genetic differentiation on this habitat type.

- Ladle, Richard, and Robert Whittaker. 2011. *Conservation biogeography*. Hoboken, NJ: Wiley-Blackwell.

This edited volume examines connections between biogeography and conservation biology, suggesting that conservation biogeography is emerging as a new subdiscipline of conservation biology. It explores how understanding biodiversity patterns can inform conservation planning and better preserve Earth's biota.

- Nagy, Laszlo, and Georg Grabherr. 2009. *The biology of Alpine habitats*. New York: Oxford Univ. Press.

The authors provide a global overview of alpine habitats and the biota they harbor, including the abiotic and biotic factors that have shaped these island-like and biodiverse habitats over ecological and evolutionary timescales.

- Schenk, John. 2013. Evolution of limited seed dispersal ability on gypsum islands. *American Journal of Botany* 100:1811–1822.

Oceanic island species often have limited dispersal ability since those islands are surrounded by unsuitable habitat into which dispersal wastes potential offspring. The author finds *Mentzelia* species endemic to gypsum soil islands have evolved relatively small-winged seeds, thus limiting their dispersal into adjacent habitats in which they are poor competitors.

- Whittaker, Robert J., and José María Fernández-Palacios. 2007. *Island biogeography: Ecology, evolution, and conservation*. 2d ed. Oxford: Oxford Univ. Press.

This book builds on the classic studies of island biogeography to show how islands have been used as model systems for studies of evolution, community ecology, etc. The book also describes island formation and environmental development to tie island geology into island biology.

Ecological Aspects

Geology and ecology are tightly linked in many cases and by many processes: [Huggett 1995](#) (cited under [General Overviews](#)) provides an excellent introduction. Climate exerts a major influence on the mineral weathering of geological substrates as well as on the composition of biological communities, and within a climate zone geological substrate often drives community characteristics. [Hahm, et al. 2013](#) provides an illustration of this principle: within a climatic zone the local composition of granite influenced vegetation, and that (by influencing erosion rates) controlled landform formation. On a large scale, geology determines climate: position on the

planet (especially latitude) is important; but also, mountains change climate through effects of elevation on temperature and rainfall. In addition, the orientation (aspect) and steepness of the surface (slope) also affect microclimates. These microclimate effects are themselves magnified as latitude increases. [Warren 2010](#) tested the relationship between aspect and microclimate variation in temperate forest herbs. The author found that the abiotic features that explained species' responses to aspect varied between the species used, showing that underlying ecological explanations for aspect responses are not universal across species. Geology influences topographic variation because different materials erode at different rates, creating landscape complexity with important effects on biological communities. As a type of rapid erosion, for example, landslides can be important geological and ecological factors in landscapes: [Walker and Shiels 2013](#) provides an excellent overview. Other geological events (such as volcanoes) also have dramatic effects on biota: [Dale, et al. 2005](#) provides a wealth of information on how the eruption of Mount St. Helens in 1980 (Oregon, United States) affected biological communities and ecosystems, as well as on how they have recovered during the intervening years. All the above factors contribute to habitat diversity and, thus, are drivers of biological diversity. [Hortal, et al. 2009](#) provides an entry point into the literature regarding links between habitat diversity and biological diversity. Geological factors also affect community productivity by influencing availability of nutrients to primary producers. [Geider, et al. 2001](#) provides a broad overview of primary productivity on Earth and its limiting factors, including nutrient supply. Geological features serve as important pools of nutrients in most nutrient cycles in ecosystems. The classic work [Vitousek 2004](#) (Hawaii, United States) illustrates connections between geological substrate and time that affect the nitrogen cycle and, through those connections, biological community function and composition. In this article, the [Biogeography](#) section explores how the spatial patterning of habitats (greatly affected by geological factors) influences biodiversity patterns, while other sections (including those on specific biological groups, e.g., [Fauna](#), etc.) provide other connections between geology and ecological topics.

- Dale, Virginia H., Frederick J. Swanson, and Charles M. Crisafulli, eds. 2005. *Ecological responses to the 1980 eruption of Mount St. Helens*. New York: Springer.

The twenty chapters in this edited volume provide a fascinating case study of the ecological effects of a famous 1980s volcanic eruption. Chapters cover responses of plant and animal communities, as well as effects on ecosystem processes.

- Geider, Richard, Evan deLucia, Paul Falkowski, et al. 2001. Primary productivity of planet earth: Biological determinants and physical constraints in terrestrial and aquatic habitats. *Global Change Biology* 7:849–882.

This broad consideration of primary production, its measurement, and its constraints in major global habitats provides context for the role of nutrient limitations in affecting this fundamental ecological process. The article also connects this topic to climate change and its potential ecological impacts.

- Hahm, W. Jesse, Clifford Riebe, Claire Lukens, and Sayaka Araki. 2013. Bedrock composition regulates mountain ecosystems and landscape evolution. *Proceedings of the National Academy of Sciences of the United States of America*.

The composition of granitic substrates in the Sierra Nevada of California, United States, is shown to be an important driver of ecosystem traits. By controlling vegetation type, substrate influences erosion rates and therefore development of landform features.

- Hortal, Joaquín, Kostas Triantis, Shai Meiri, Elisa Thébault, and Spyros Sfenthourakis. 2009. Island species richness increases with habitat diversity. *American Naturalist* 174:E205–E217.

In this review of the well-established positive relationship between habitat diversity and species richness, the authors examine the exact shape of the relationship and relate habitat diversity/species richness relationships to theoretical models of niche breadth.

- Vitousek, Peter. 2004. *Nutrient cycling and limitation: Hawai'i as a model system*. Princeton, NJ: Princeton Univ. Press.

Summarizing two decades of research, this award-winning book illustrates the importance of nutrient cycles to biological communities, including how time since island formation affects nutrient cycles, and through them, community composition.

- Walker, Lawrence, and Aaron Shiels. 2013. *Landslide ecology*. Cambridge, UK: Cambridge Univ. Press.

An excellent entry point into the literature on landslides, including connections between geological and biological phenomena as well as the impacts of landslides on human activities (and vice versa). The authors summarize landslide impacts on a wide range of organisms as well as impacts on ecological processes.

- Warren, Robert. 2010. An experimental test of well-described vegetation patterns across slope aspects using woodland herb transplants and manipulated abiotic drivers. *New Phytologist* 185:1038–1049.

After describing how aspect became recognized as an important ecological factor, the author investigates the abiotic factors responsible for aspect effects. He finds that the abiotic explanation depends on both species and its growth stage, and concludes that generalizations about abiotic drivers of aspect effects are difficult to make.

Evolutionary Aspects

Within a given climatic region, geological differences play a fundamental role in generating habitat heterogeneity, resulting in local adaptation and population differentiation leading to plant speciation. [Kruckeberg 1986](#) and [Rajakaruna 2004](#) explore the modes and mechanisms of speciation under the geodaphic influence using model plants from western North America. The study of ecological speciation, including that stemming from geodaphic influences, has long interested plant ecologists. [Turesson 1922](#) and [Clausen, et al. 1940](#) are two 20th-century classics of evolutionary ecology, describing how experimental methods such as common garden and reciprocal transplant studies can be used to examine the roles played by phenotypic plasticity and

local adaptation in habitat specialization. Plants endemic to serpentinite-derived substrates have been effective models for the study of edaphically driven speciation. Several chapters in [Harrison and Rajakaruna 2011](#) explore key topics in the evolutionary process, including intraspecific variation, local adaptation, and modes of speciation using plants adapted to serpentinites of California. Additional chapters examine genomic and phylogenetic approaches to the study of plant speciation under the geodaphic influence. Although restricted to serpentinite-plant associations, [Brady, et al. 2005](#) is another excellent resource for evolutionary topics relating to substrate endemism. The roles that extreme habitats—such as oceanic pillow lavas, evaporitic settings, microbialites, stromatolites, and other deep subsurface and seafloor environments—play in the evolution of microbial life also have attracted much attention in the early 21st century. [Dilek, et al. 2008](#) is a useful resource for the study of extremophilic microbes in extreme geochemical settings. Macroevolutionary aspects of life through time, particularly of animal species, are often interpreted using the fossil record. [Patzkowsky and Holland 2012](#) is an authoritative treatment of how the distribution of fossil taxa in time and space is controlled not only by processes of ecology, evolution, and environmental change, but also by the stratigraphic processes that govern when and where fossil-containing sediment is deposited and preserved. For a broad overview of geodaphic influences on the ecology and evolution of plant and animal species and the assembly of their communities, see [Huggett 1995](#) (cited under [General Overviews](#)).

- Brady, Kristy U., Arthur R. Kruckeberg, and Harvey D. Bradshaw Jr. 2005. Evolutionary ecology of plant adaptation to serpentine soils. *Annual Review of Ecology, Evolution, and Systematics* 36:243–266.

This review covers the defining features of serpentinite-derived soils and the mechanisms proposed for serpentinite tolerance. It also addresses the evolution and genetics of serpentinite adaptation and how speciation may occur under its influence.

- Clausen, Jens C., David D. Keck, and William M. Hiesey. 1940. *Experimental studies on the nature of species*. Vol. 1, *Effects of varied environments on western North American plants*. Carnegie Institution of Washington Publication 520. Washington, DC: Carnegie Institution of Washington.

Foundational research in plant evolutionary ecology is contained in this publication (and several others) on experimental studies into the nature of intraspecific variation. Using experimental approaches they explore the genetic and environmental control of phenotypic traits in western North American species of *Potentilla*, *Achillea*, *Horkelia*, *Penstemon*, and *Artemisia*, among others.

- Dilek, Yildirim, Harald Furnes, and Karlis Muehlenbachs, eds. 2008. *Links between geological processes, microbial activities and evolution of life: Microbes and geology*. Dordrecht, The Netherlands: Springer.

The ten chapters explore the mode and nature of associations between geological processes and microbial activities, and their significance for the origin and evolution of life on Earth. Topics include microbial adaptation and evolution in extreme environments

such as oceanic pillow lavas, hyaloclastites, deep subsurface, sub-seafloor, and Bahamian stromatolites.

- Harrison, Susan P., and Nishanta Rajakaruna, eds. 2011. *Serpentine: The evolution and ecology of a model system*. Berkeley: Univ. of California Press.

The nineteen chapters discuss how metal-enriched serpentinite habitats have been used or can be used to address major questions in Earth history, evolution, ecology, conservation, and restoration. Relevant evolutionary topics include intraspecific variation and local adaptation, speciation, phylogenetic analyses of endemism, and genomic approaches to the study of adaptation.

- Kruckeberg, Arthur R. 1986. An essay: The stimulus of unusual geologies for plant speciation. *Systematic Botany* 11:455–463.

Using western North America taxa as model systems, the paper describes possible modes of evolutionary diversification under the geodaphic influence. Although the focus is on plant-serpentinite relations, the modes and mechanisms of population differentiation and speciation outlined in the paper are generally applicable to species undergoing ecological divergence.

- Patzkowsky, Mark E., and Steven M. Holland. 2012. *Stratigraphic paleobiology: Understanding the distribution of fossil taxa in time and space*. Chicago: Univ. of Chicago Press.

The authors explore the exciting possibilities of stratigraphic paleobiology and demonstrate its great potential to examine critical questions about the history of life on Earth. The chapters provide an analytical framework for assessing the fossil record and paleontological literature by employing the principles of sediment accumulation.

- Rajakaruna, Nishanta. 2004. The edaphic factor in the origin of species. *International Geology Review* 46:471–478.

The relationship between adaptation to substrate and the origins of reproductive isolation is examined using ecologically divergent populations of western North American species of *Mimulus* and *Lasthenia*. The review makes a strong case for geodaphically driven speciation in flowering plants.

- Turesson, Göte. 1922. The species and the variety as ecological units. *Hereditas* 3.1: 100–113.

This foundational classic on the nature of intraspecific variation in plant species provides one of the earliest discussions of the ecotypic concept. The term ecotype, coined by the author, is used as an ecological subunit arising from genotypical response of a species to a particular habitat.

Physiology and Genetics

The study of the physiology and genetics of traits conferring adaptation to extreme geodaphic settings is a fast-developing area of research. Early-21st-century studies have shed light on novel physiological mechanisms for abiotic stress tolerance and their underlying genetic bases, providing tools for biotechnological applications in fields such as agriculture, forestry, and reclamation. In this regard, much attention has been directed at genetically modifying domesticated plants and animals (as well as microbes) to deal with abiotic stress, including stressors associated with climate change–related influences and geodaphic factors. [Jenks and Hasegawa 2014](#) is an excellent source for information on the physiology and genetics of plant adaptations to abiotic stressors such as salinity, flooding, temperature, and drought, while [Willmer, et al. 2004](#) is a useful resource for information on tolerance to heat, cold, salinity, and drought in animal species, including molecular insights into the mechanistic bases of adaptations to abiotic stressors animals encounter in various geodaphic settings. [Pointing and Belnap 2012](#) explores stress tolerance in microbes, particularly those exposed to cold and hot deserts: habitats that cover large portions of the world. The authors' review discusses adaptations that confer tolerance to water stress in soil- and rock-colonizing species of cyanobacteria, chlorophytes, fungi, and heterotrophic bacteria. Tolerance to toxic heavy metals (often associated with anthropogenic contamination) has been a major area of research in the early 21st century. [Janssens, et al. 2009](#) reviews molecular mechanisms associated with heavy metal tolerance in invertebrate species, with a focus on physiological mechanisms of cadmium tolerance in springtails. [DalCorso, et al. 2013](#) discusses the state-of-the-field for research in metal tolerance and accumulation, highlighting advances made due to methods such as transcriptomic-based DNA microarrays and proteomics. [Pérez-Clemente, et al. 2013](#) and [von Wettberg and Wright 2011](#) are excellent sources for advances in biotechnological methodology to investigate physiological and genetic bases for adaptations to edaphic stressors, including salinity and heavy metals. A chapter in [Rodriguez, et al. 2012](#) explores the role fungi play in conferring plant tolerance to abiotic stressors including drought, temperature, and salinity. This chapter, along with others included in the book, emphasizes the importance of paying attention to fungi in the study of plant geocology.

- dalCorso, Giovanni, Elisa Fasani, and Antonella Furini. 2013. [Recent advances in the analysis of metal hyperaccumulation and hypertolerance in plants using proteomics](#). *Frontiers in Plant Science* 4: Article ID 280.

This review is an excellent source of information regarding molecular pathways of heavy metal tolerance in metal hyperaccumulator and hypertolerant species. The focus is on advances in transcriptomic-based DNA microarrays and proteomics in the study of metal tolerance in plants.

- 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 insects and other invertebrates, highlighting research on metallothioneins and how their overexpression promotes cadmium tolerance in springtails (Collembola).

- Jenks, Matthew A., and Paul M. Hasegawa, eds. 2014. *Plant abiotic stress*. 2d ed. Ames, IA: Wiley.

The ten chapters in this comprehensive treatment on the physiology and genetics of plant adaptations to abiotic stresses (such as salinity, flooding, temperature, and drought) are written by experts in respective fields. Topics also include genomic approaches to the study of stress tolerance and epigenetic impacts on abiotic stress tolerance.

- Pérez-Clemente, Rosa M., Vicente Vives, Sara I. Zandalinas, María F. López-Climent, Valeria Muñoz, and Aurelio Gómez-Cadenas. 2013. Biotechnological approaches to study plant responses to stress. *BioMed Research International*. Article ID 654120.

The review summarizes progress on techniques in the study of plant responses to abiotic and biotic stress. Methods discussed include approaches in genomics, proteomics, metabolomics, and transgenic-based techniques. The importance of such biotechnological advances in stress tolerance to agricultural practices is also emphasized.

- Pointing, Stephen B., and Jayne Belnap. 2012. Microbial colonization and controls in dryland systems. *Nature Reviews Microbiology* 10:551–562.

The review illustrates the nature of microbial colonization in hot and cold deserts, and the adaptations that are important for the survival of soil- and rock-community associated microbes, including cyanobacteria, chlorophytes, fungi, and heterotrophic bacteria. Microbial influences in geochemical processes and microbial recovery and management are also a focus.

- Rodriguez, Russell J., Claire J. Woodward, and Regina S. Redman. 2012. Fungal influence on plant tolerance to stress. In *Biocomplexity of plant-fungal interactions*. Edited by Darlene Southworth, 155–163. Oxford: Wiley-Blackwell.

The role of fungi in plant tolerance to stresses such as drought, temperature, and salt is the focus of this chapter. Mechanisms of symbiotically conferred stress tolerance point to the fundamental role that soil microbes, such as fungi, play in tolerating edaphic and other abiotic stresses plants encounter in their habitats.

- von Wettberg, Eric, and Jessica W. Wright. 2011. Genomic approaches to understanding adaptation. In *Serpentine: The evolution and ecology of a model system*. Edited by Susan P. Harrison and Nishanta Rajakaruna, 139–154. Berkeley: Univ. of California Press.

The chapter describes advances in the fields of ionomics, metabolomics, proteomics, transcriptomics, and genomics that can be utilized to uncover the mechanistic and genetic

basis for the tolerance of and adaptation to serpentinite- and other heavy metal-enriched soils.

- Willmer, Pat, Graham Stone, and Ian Johnston. 2004. *Environmental physiology of animals*. 2d ed. Oxford: Wiley-Blackwell.

The seventeen chapters explore all aspects of abiotic stress tolerance in animals, providing excellent summaries of tolerance to stresses associated with both terrestrial and aquatic environments. Discussions on tolerance to heat, cold, salinity, and drought are particularly relevant as well as molecular insights into the mechanistic bases of adaptations.

Reclamation and Restoration

Humanity's destruction of biological communities can be ameliorated by reclamation and restoration. Restoration ecology is a burgeoning and relatively new field: [van Andel and Aronson 2012](#) is a good introduction to the discipline and its goals, methods, and challenges. Geological considerations are important to reclamation and restoration efforts. For example, [Montgomery 2004](#) points out that, at the landscape level, geology and geomorphology are particularly important considerations in restoration of salmon runs. Particular geological substrates present special problems for restoration because they are inhabited by species or populations adapted to those substrates: the section on [Evolutionary Aspects](#) explores how geology can affect evolution on unusual substrates to produce locally adapted populations or species. As an example of these special restoration problems, [O'Dell and Claassen 2011](#) provides an overview of challenges and approaches useful for reclamation or restoration of serpentine sites. As with restoration of most sites on unusual geological materials, revegetation of serpentine sites should use plant materials obtained from populations that are adapted to those soils. In another example, [Gilardelli, et al. 2013](#) studies natural succession and restoration techniques on limestone quarries, illustrating the common positive correlation between economic expense and revegetation success. Fortunately, [Tropek, et al. 2010](#) points out that even spontaneous succession can be valuable for conservation objectives. There have been attempts to create sites functionally similar to those on special substrates on sites with normal soils. [Bonebrake, et al. 2011](#) attempted to modify nonserpentine soils to create soils similar to serpentine, and thus host their specialized flora (and discourage colonization by nonnative plants). They were only partly successful, demonstrating that such edaphic manipulation to date has limited application to restoration ecology. Geoengineering is a new field that proposes to manipulate Earth's ecological systems to reverse unintended changes caused by human activities. For example, [Caldeira, et al. 2013](#) summarizes proposals to address global climate change through geoengineering activities. The review [Power, et al. 2013](#) summarizes one potential geoengineering technique, showing how serpentinite may be used to sequester carbon dioxide. This technology takes advantage of the fact that carbonate minerals are produced during hydrothermal altering of serpentinite. Carbon could be sequestered by mining serpentinite for use in chemical reactors, or by injecting carbon dioxide solutions directly into serpentinite deposits. Large-scale implementation of these activities on serpentine landscapes, however, may create conservation challenges (see section on [Conservation](#)).

- Bonebrake, Timothy, Ryan Navratil, Carol Boggs, Scott Fendorff, Christopher Field, and Paul Ehrlich. 2011. Native and non-native community assembly through edaphic manipulation: Implications for habitat creation and restoration. *Restoration Ecology* 19:709–716.

The authors attempted to manipulate nonserpentine soils to create conditions that mimic serpentine soils, and thus could be useful for conservation of serpentine-associated plants and animals. They were only partially successful, pointing to the difficulty of artificially creating specialized edaphic conditions and the importance of preservation of natural systems.

- Caldeira, Jen, Govindasamy Bala, and Long Cao. 2013. The science of geoengineering. *Annual Review of Earth and Planetary Sciences* 41:231–256.

A review of proposals to address Earth’s recent human-induced climate change through planetary-scale actions, including approaches to modify solar input as well as change atmospheric carbon dioxide concentrations.

- Gilardelli, Federica, Sergio Sgorbati, Sandra Citterio, and Rodolfo Gentili. 2013. Restoring limestone quarries: Hayseed, commercial seed mixture or spontaneous succession? *Land Degradation and Development*.

Illustrating the importance of how restoration “success” is defined, this study compares several methods of quarry restoration. Using a cost-benefit analysis, and defining success to include high biodiversity, the authors conclude that the most expensive method produces the best restoration success.

- Montgomery, David R. 2004. Geology, geomorphology, and the restoration ecology of salmon. *GSA Today* 14.11: 4–12.

This article describes how geology and geomorphology are vital components of the habitat of salmon and how these factors must be considered in efforts to restore salmon runs. It also provides a good entry into the literature regarding salmon ecology and restoration programs.

- O’Dell, Ryan E., and Victor Claassen. 2011. Restoration and revegetation of harsh soils. In *Serpentine: Evolution and ecology in a model system*. Edited by Susan P. Harrison and Nishanta Rajakaruna, 383–416. Berkeley: Univ. of California Press.

The chapter focuses on the restoration and revegetation of heavy metal–enriched serpentine sites. The authors summarize soil and vegetation manipulation methods used to restore degraded serpentine soil communities, and focus on critical steps needed for successful revegetation of degraded serpentine and other edaphically harsh settings.

- Power, Ian M., Siobhan A. Wilson, and Gregory M. Dipple. 2013. Serpentinite carbonation for CO₂ sequestration. *Elements* 9:115–121.

This review explains the process of carbonation using minerals found in serpentine areas. It explains how serpentine minerals could be used to sequester CO₂ at both local and global scales using either in situ or ex situ technologies.

- Tropek, Robert, Tomas Kadlec, Petra Karesova, et al. 2010. Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants. *Journal of Applied Ecology* 47:139–147.

This report shows that while technical restoration usually accelerates revegetation of mining sites, spontaneously recovering sites may provide better habitat for some species of conservation concern. Thus a mix of restoration techniques may be a preferred restoration strategy.

- van Andel, Jelte, and James Aronson, eds. 2012. *Restoration ecology: The new frontier*. 2d ed. Malden, MA: Blackwell Science.

This edited volume provides an overview of concepts and ecological underpinnings of restoration ecology, along with eight chapters that target restoration of particular types of freshwater and terrestrial communities.

Climate Change Consequences

Climate change is a major challenge to global biodiversity. [Cowie 2012](#) provides a comprehensive overview of the evidence regarding climate change, its causes and consequences for humans and other organisms, and potential actions to address it. Climate change impacts on biodiversity may be especially large for species with geographically restricted or patchy distributions because, as climate changes, their habitat may disappear or be significantly altered. For example, low islands are very vulnerable to sea level rise. [Wetzel, et al. 2013](#) predicted major conservation impacts of sea level rise in Southeast Asia and Pacific regions. Effects of climate change are especially rapid in Arctic regions. Shrinkage of the extent of pack ice (an important habitat feature of mammals such as polar bears) is an example, and [Gormezano and Rockwell 2013](#) discusses changes in the diet of polar bears from the Hudson Bay area that are occurring as pack ice distribution changes. In mountainous regions, upward movement of climate zones may impact species. Exemplifying this threat is the American pika, found at high elevations in western North America. Upward shifts of mountain communities may cause the species' habitat to disappear in some locations: [Beever, et al. 2011](#) reports that the species is already experiencing local population extinctions and its range is shifting rapidly upward. Another challenge is if favorable climatic conditions move to areas to which a species cannot disperse, or to which a species cannot disperse rapidly enough. [Damschen, et al. 2012](#) uses species distribution models to examine extinction risk for plant species endemic to serpentine soil islands, but find surprisingly little extinction risk. However, the authors point out that many factors (including species' dispersal ability and the geographic distribution of soil islands) can affect this outcome. The section on [Biogeography](#) provides additional information regarding those factors. Climate change will likely affect biodiversity, but [Gilman, et al. 2011](#) points out that more diverse communities may be better able to withstand changes brought about by climate change. Finally, biologists often focus on the direct responses of organisms to climate change,

but how humans respond to climate change may produce important indirect effects on biodiversity. Building on the example above of sea level rise effects on islands, [Wetzel, et al. 2012](#) shows that movements of human refugees in response to rising sea levels may have greater impacts on some species than the direct effects of sea level changes themselves.

- Beever, Erik, Chris Ray, Jenifer Wilkening, Peter Brussard, and Philip Mote. 2011. Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology* 17:2054–2070.

Using distribution records spanning a century, the authors document extinction and upward range expansion of the American pika in western North American mountains, illustrating the effects of climate change on montane species and communities.

- Cowie, Jonathan. 2012. *Climate change: Biological and human aspects*. 2d ed. Cambridge, UK: Cambridge Univ. Press.

This book provides an early-21st-century introduction to climate change past and present, including information on its impacts on humans and other organisms, its projected impacts, and efforts to address those impacts.

- Damschen, Ellen, Susan Harrison, David Ackerly, Barbara Fernandez-Going, and Brian Anacker. 2012. Endemic plant communities on special soils: Early victims or hardy survivors of climate change? *Journal of Ecology* 100:1122–1130.

The authors use species distribution models to predict the response of serpentine endemic species to climate change in California, United States, postulating high extinction risk. They find relatively little extinction risk, and provide a literature review that can guide future explorations of climate change on special soils.

- Gilman, R. Tucker, Nicholas Fabina, Karen Abbott, and Nicole Rafferty. 2011. Evolution of plant-pollinator mutualisms in response to climate change. *Evolutionary Applications* 5.1: 2–16.

The authors use a modeling approach to study how changes in flowering time might impact plant-pollinator mutualisms. Among other conclusions, they find that more diverse pollinator communities buffer climate change effects, thus providing a benefit of maintaining pollinator biodiversity.

- Gormezano, Linda, and Robert Rockwell. 2013. What to eat now? Shifts in polar bear diet during ice-free season in western Hudson Bay. *Ecology and Evolution* 3:3509–3523.

The authors compare diets by comparing contents of scat collected in 2010 to scat collected forty years prior. They find diets have shifted as bears have adjusted to shrinkage of pack ice, but whether the species will be able to survive continued habitat changes is an actively debated issue.

- Wetzel, Florian, Helmut Beissmann, Dustin Penn, and Walter Jetz. 2013. Vulnerability of terrestrial island vertebrates to projected sea-level rise. *Global Change Biology* 19:2058–2070.

Using sea level rise projections and species distribution models, the authors estimate impacts of sea level rise on island species in Southeast Asia and Pacific areas. They find some island species are particularly susceptible to this threat and may become extinct as a result.

- Wetzel, Florian, W. Daniel Kissling, Helmut Beissmann, and Dustin Penn. 2012. Future climate change driven sea-level rise: Secondary consequences from human displacement for island biodiversity. *Global Change Biology* 18:2707–2719.

This study shows that sea level rise may have important effects on biodiversity because movements of humans in response to sea level changes will likely impact animal habitats, and thus create important secondary effects on biodiversity.

Conservation

Unusual geological substrates may harbor unique populations or species (see [Evolutionary Aspects](#)). Detecting unique biological elements is the first step toward their conservation: [Lin and Li 2014](#) describes five new species of armored spider from caves in Chinese karst habitat. [Wulff, et al. 2013](#) examines the flora of New Caledonia, finding that geological substrate is an important characteristic for species with few populations. The authors use species distribution models to predict locations of new populations and identify areas for conservation attention. Human uses of special substrates can put unique biological elements at risk: [Jacobi, et al. 2011](#) illustrates this threat for plants in metal-mining areas of Brazil. While special geological substrates may be difficult for exotic species to colonize, exotics can create conservation problems in these areas. [Vallano, et al. 2012](#) demonstrates that human-caused nitrogen deposition may, by increasing fertility of serpentine soils and thus shifting competitive relationships to favor nonnatives, promote invasion by exotics. Besides invasion by nonadapted exotics, sites with special substrates may be vulnerable to invasion by exotics native to those substrates in other areas of the globe. This is a concern regarding the use of nonnative species in habitat restoration projects (see [Reclamation and Restoration](#)). An example is the case of smooth cordgrass, a native of eastern North American salt marshes used for salt marsh restoration in other areas (it also has spread accidentally). Effects in nonnative areas are mixed. For example, [Ma, et al. 2013](#) reports that in China, cordgrass promotes the spread of a threatened bird species that uses the grass as a nesting and feeding site. In contrast, [Nordby, et al. 2009](#) describes stands of introduced cordgrass as an ecological trap for a rare marsh sparrow subspecies (because it attracts birds to sites where nests are often destroyed by high tides). On a broader scale, geocology is an important consideration for management of protected areas. [Gordon, et al. 2002](#) points out how substrate affects ecology and management of alpine zones of several European mountain ranges, while [Montgomery 2004](#) (cited under [Reclamation and Restoration](#)) shows the importance of geological features in restoration of salmon runs. Another important conservation challenge is construction of networks of protected areas to preserve biodiversity. This issue is particularly important to conservation in geologically unusual areas, given the fragmented nature

of many of these habitats (see [Biogeography](#)). [Clements, et al. 2006](#) describes the fascinating case of limestone karsts in Southeast Asia, showcasing their unique endemic fauna and flora as well as the conservation challenges facing their preservation.

- Clements, Reuben, Navjot Sodhi, Menno Schilthuizen, and Peter King. 2006. Limestone karsts of Southeast Asia: Imperiled arks of biodiversity. *BioScience* 56.9: 733–742.

The authors describe the geology, flora and fauna, human uses, and conservation challenges facing these often-spectacular formations. This article is an excellent example of the opportunities and difficulties for conservation of geologically unusual areas.

- Gordon, John E., Igor J. Dvorač, Christer Jonasson, Melanie Josefsson, Milena Kociánová, and Des B. A. Thompson. 2002. Geo-ecology and management of sensitive montane landscapes. *Geografiska Annaler: Series A, Physical Geography* 84:193–203.

Comparing three European alpine areas (in Scotland, Czech Republic, and Sweden), the authors demonstrate how consideration of geoecological factors can inform management to protect biodiversity and address various human impacts such as deforestation, grazing, pasturing, recreation, pollution, and climate change.

- Jacobi, Claudia, Flávio do Carmo, and Iara de Campos. 2011. Soaring extinction threats to endemic plants in Brazilian metal-rich regions. *AMBIO* 40:540–543.

The authors point to the lack of protection of endemic plant species often found in areas targeted by mining operations in Brazil. They also point out the responsibility of countries that have signed the Convention on Biological Diversity to inventory and protect their biodiversity.

- Lin, Yucheng, and Shuqiang Li. 2014. New cave-dwelling armored spiders (Araneae, Tetrablemmidae) from Southwest China. *ZooKeys* 388:35–76.

Describing five new species of armored spider in a new genus, the authors illustrate the potential for discovery of new species in geologically unusual areas, in this case caves in a limestone karst area of China.

- Ma, Zhijun, Xiaojing Gan, Chi-Yeung Choi, and Bo Li. 2013. Effects of invasive cordgrass on presence of Marsh Grassbird in an area where it is not native. *Conservation Biology* 28:150–158.

The authors show that smooth cordgrass provides suitable habitat for a rare bird species that is spreading into these marsh habitats, providing new areas for occupancy for the bird and thus providing at least some conservation benefit.

- Nordby, J. Cully, Andrew Cohen, and Steven Beissinger. 2009. Effects of a habitat-altering invader on nesting sparrows: An ecological trap? *Biological Invasions* 11:565–575.

A case study showing that a rare sparrow is attracted to dense stands of smooth cordgrass as nest sites, but these stands occur relatively low in the salt marsh topographic profile and thus are prone to being destroyed by flooding during high tide events.

- Vallano, Dena M., Paul C. Selmants, and Erika S. Zavaleta. 2012. Simulated nitrogen deposition enhances performance of an exotic grass relative to native serpentine grassland competitors. *Plant Ecology* 213:1015–1026.

Deposition of nitrogen may cause serpentine habitats to be more susceptible to invasion by nonnative, nonserpentine species. The authors show that nitrogen deposition may shift the competitive relationship between an invasive and native plant species so that the invasive is favored.

- Wulff, Adrien, Peter Hollingsworth, Antje Ahrends, et al. 2013. Conservation priorities in a biodiversity hotspot: Analysis of narrow endemic plant species in New Caledonia. *PLoS ONE* 8.9: e73371.

Finding that geological substrate is an important feature for species with narrow endemic status, the authors use species distribution models to map areas for conservation protection and to identify species under potential threat from mining operations.

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Geoecology

[Nishanta Rajakaruna](#), [Robert S. Boyd](#)

Introduction

Geology plays a fundamental role in shaping the biotic world around us. Geologic history (plate tectonics and orogenic or mountain-building activity), landforms (geomorphology), and lithology (parent material and substrate) influence ecological and evolutionary processes and contribute to both macro- and micro-scale patterns of biogeography. Geocology is an interdisciplinary and multidisciplinary science that integrates the geosciences with the life sciences, focusing on the myriad influences of geological processes on historical and contemporary patterns of biogeography, including the causes and consequences of geodaphics on biota at all temporal and spatial scales. At the same time, geocology examines the role biota play in a range of geodaphic processes, including in weathering and pedogenesis, thereby altering the chemical and physical composition of the Earth's surface and its patterns of biodiversity. Geobiology (geobotany and geozoology), biogeography, and biogeochemistry are important subfields within geocology. Much of earth's biotic heterogeneity is a direct result of ecological heterogeneity stemming from geodaphic influences. Early naturalists often associated the occurrence of certain plant species with particular geologies, leading to biogeochemical prospecting for highly sought after minerals and metals. Recent advances in biogeochemical studies have led to phytomining, the use of plants to extract metals such as nickel and gold from metal-enriched soils. Plant evolutionary ecology also has its roots in geocology, with pioneering experimental studies highlighting the influence of landforms and geodaphics on plant fitness and the evolutionary process, leading to the development of the concept of ecotypes—genetically distinct populations that are locally adapted to specific habitats characterized by distinct environmental conditions. Chemically imbalanced (i.e., nutrient poor or metal rich) geologic materials, such as serpentinites, contribute greatly to biodiversity, with high levels of plant endemism in regions overlying such geologies. Study of these endemic plants has contributed to ecological and evolutionary theory as well as basic and applied aspects of conservation and restoration sciences. Recent advances in geographic information science (GIS) and remote sensing, including light detection and ranging (LiDAR) and satellite imagery, combined with advanced computational techniques, have also provided means to closely monitor changes in patterns and processes of biota spread across geologic, topographic, and related ecological gradients. Such advances have led to effective conservation planning and better management of threats to biota resulting from stressors associated with climate change.

General Overviews

Geocology is the study of the multifaceted relationships that exist between substrate and biota. Parent materials, climate, topography, and time determine the kind of substrate that becomes available for colonization by biota, and their habitation further influences the nature of the substrate upon which plants grow and animals and microbes dwell. Humans have long observed the special associations between organisms and their substrate, and such knowledge has served as the foundation of biogeoprospecting, the use of organisms as indicators of minerals and chemical elements found within geologic material. [Martin and Coughtrey 1982](#) and [Brooks 1983](#) (cited under [Flora](#)) are excellent resources for the early literature on this topic, particularly in Europe. [Huggett 1995](#) is an authoritative treatment of geocology, providing an extensive discussion on the roles that climate, geology, soils, altitude, topography, insularity, and disturbance play in generating and maintaining patterns of biotic diversity. [Knoll, et al. 2012](#) is also a good resource for a solid foundation on geobiological topics, including the role of nutrient cycles in biological processes and biota as geobiological agents, in addition to information on

geobiological weathering, paleogeobiology, and technological advances in geobiological research. Much of the research on geocology has focused on microbe- and plant-substrate relations. [Konhauser 2006](#) is an excellent introduction to the geocology of microbes, while [Kruckeberg 2002](#) is a comprehensive treatment on the roles that geology, topography, and geologic history play in shaping plant communities. Some plant-geology interactions have received more attention than others, particularly on serpentinites, due to their hosting unique communities containing a high proportion of endemic and rare species. [Roberts and Proctor 1992](#) is an early but comprehensive treatment on the ecology of serpentinite-associated plants. [Alexander, et al. 2007](#) explores the substrate-biota relationships for the serpentinites of western North America, a region that has been the focus of geocological investigations since the mid-1900s. For recent treatments on the ecology and evolution of serpentinite habitats, see [Brady, et al. 2005](#) and [Harrison and Rajakaruna 2011](#) (both cited under [Evolutionary Aspects](#)). Unlike studies for plants and microbes, studies examining the role of lithology on animals are relatively scarce (but see citations under [Fauna](#)). Animal studies typically focus on how geologic history and landforms (and associated climatic conditions) influence animal ecology and evolution. [Barrett and Peles 1999](#) is a good introductory resource for such information, including how landscape patterns and processes impact small mammals and how they, in turn, influence landscape structure and composition.

- Alexander, Earl B., Robert G. Coleman, Todd Keeler-Wolf, and Susan P. Harrison. 2007. *Serpentine geocology of western North America: Geology, soils and vegetation*. New York: Oxford Univ. Press.

This book explores the ecology of serpentinite rock outcrops in western North America, focusing on soils and plants but including information on other organisms, including animals, fungi, and other microorganisms where feasible.

- Barrett, Gary W., and John D. Peles, eds. 1999. *Landscape ecology of small mammals*. New York: Springer.

The fifteen chapters discuss case studies, providing new insights into how landscape patterns and processes impact small mammals and how small mammals, in turn, influence landscape structure and composition.

- Huggett, Richard J. 1995. *Geocology: An evolutionary approach*. New York: Routledge.

The nine chapters introduce the reader to the structure and function of geoecosystems, their components, and their environment. The roles that climate, soils, geology, altitude, topography, insularity, and disturbance play in shaping biotic communities are a central focus of this book.

- Knoll, Andrew H., Donald E. Canfield, and Kurt O. Konhauser, eds. 2012. *Fundamentals of geobiology*. Oxford: Wiley-Blackwell.

The book is a thorough introduction to the use of molecular tools and stable isotopes in geobiological research, and to geobiology and associated topics such as the role of

carbon, nitrogen, and other nutrient cycles in biological processes; geochemical origins of life; paleogeobiology; microbes; plants; animals; and humans as geobiological agents.

- Konhauser, Kurt O. 2006. *Introduction to geomicrobiology*. Malden, MA: Blackwell Science.

The seven chapters provide a comprehensive review of the role microbes play in shaping Earth's physical environments. Topics include biomineralization, microbial weathering, microbial role in contaminant mobility, bioremediation and biorecovery, the function of microorganisms in mineral dissolution and oxidation, and Earth's early microbial life, among others.

- Kruckeberg, Arthur R. 2002. *Geology and plant life: The effects of landforms and rock types on plants*. Seattle: Univ. of Washington Press.

The book explores the roles landforms, lithology, and geologic histories play in generating and maintaining plant diversity. It reviews the rich history of geobotanical studies; discusses geodaphic influences on plant life, including in ecological and evolutionary processes; and provides an overview of human influences on the geology-plant interphase.

- Martin, Michael H., and Peter J. Coughtrey. 1982. *Biological monitoring of heavy metal pollution: Land and air*. Dordrecht, The Netherlands: Springer.

Although published in the 1980s, the eight chapters provide an excellent overview of the historic and current uses of plants and animals to detect heavy metals in both natural and anthropogenic settings. The primary focus is on the use of plants as effective monitors of heavy metals in rocks, soils, and air.

- Roberts, Bruce A., and John Proctor, eds. 1992. *The ecology of areas with serpentinitized rocks: A world view*. Geobotany 17. Dordrecht, The Netherlands: Kluwer Academic.

After a brief geological review, thirteen contributed chapters cover serpentinite ecology in areas within North America, Europe, Africa, Australia, and Asia. Coverage reflects the limited state of knowledge at the time, but the book is a good entry point into the pre-1990s serpentinite ecology literature.

Journals

Papers regarding geoecology can be found in a variety of journals because this multidisciplinary and interdisciplinary topic is pertinent to many academic fields, including biogeochemistry, geobiology, biogeography, landscape ecology, evolution, conservation, and restoration. Important journals that publish papers involving geoecology include [Journal of Biogeography](#), [Global Ecology and Biogeography](#), and [Diversity and Distributions](#). All three journals frequently publish papers dealing with the roles played by geology and soil conditions in spatial, ecological, and historical biogeography of organisms. [Plant and Soil](#) publishes papers on all aspects of soil-

plant interactions, including those examining how soil conditions contribute to local, regional, and global plant distributions. [*Geobiology*](#) is an interdisciplinary journal focusing on the relationships between biology and Earth's physical and chemical environment, while [*Geomicrobiology Journal*](#) explores aspects of microbial transformation of geologic materials and the impact such alterations have had on Earth and its biota through time. [*Journal of Geographic Information System*](#) and [*International Journal of Geographical Information Science*](#) publish basic and applied research on computational methods, including geographic information science (GIS) and light detection and ranging (LiDAR), available for the study of biotic patterns in both natural and anthropogenic landscapes. Approaches to the study of geocology are diverse and are carried out worldwide and, thus, papers associated with geocological topics can be found in numerous international journals; we have listed a few important journals publishing original research and comprehensive reviews on geocological topics.

- [*Diversity and Distributions*](#). 1993–.

The focus of this journal includes papers dealing with the application of biogeographical principles, theories, and analyses to problems concerning the conservation of biodiversity.

- [*Geobiology*](#). 2003–.

The journal publishes papers on the relationships between life and Earth's chemical and physical environments, especially papers that contain both geological and biological elements.

- [*Geomicrobiology Journal*](#). 1978–.

The journal publishes research and review articles on microbial transformations of materials composing Earth's crust, focusing on bacteria, yeasts, filamentous fungi, microalgae, protists, and related microorganisms as geomechanical or geochemical agents.

- [*Global Ecology and Biogeography*](#). 1991–.

The journal publishes studies exploring broad and consistent patterns in the ecological characteristics of organisms and ecosystems, particularly those addressing general ecological hypotheses, using data of broad geographic, taxonomic, or temporal scope.

- [*International Journal of Geographical Information Science*](#). 1987–.

The journal provides a venue for papers on approaches, methods, and research relating to GIS. Research on the design, implementation, and use of GIS for monitoring species, predicting patterns of species distributions, and decision making for effective conservation planning and urban design is regularly published here.

- [*Journal of Biogeography*](#). 1974–.

The journal publishes original research papers and reviews dealing with all aspects of spatial, ecological, and historical biogeography. The journal is the primary source for biogeographical studies carried out globally, using recent advances in geocological research.

- [*Journal of Geographic Information System*](#). 2009–.

The journal frequently publishes theoretical and applied research on the use of GIS, high performance computing, and remote sensing methods such as LiDAR in detecting and analyzing distributional patterns of biota, especially vegetation, in natural and anthropogenic habitats.

- [*Plant and Soil*](#).

This journal covers fundamental and applied aspects of plant-soil interactions, including how differences in soil conditions contribute to differences in plant distributions. Additional topics include plant-soil-microbe relations.

Geologic, Pedologic, and Biotic Influences and Interactions

Geologic and pedologic processes greatly influence the ecology and evolution of biota. Vicariant events including plate tectonics, orogenic activities, and oceanic island formations lead to disjunctions in biota, contributing to geographic isolation and subsequent speciation. Further, they influence both regional and global patterns of biodiversity. The complex relationships between organisms and their substrate also involve interactions that affect both the substrate and its ecology. [Wardle 2006](#) stresses the need for examining aboveground biotic drivers of soil biodiversity to better understand community and ecosystem ecology and relationships between biodiversity and ecosystem functioning. For example, soil crust-forming microbes exert a strong influence on water infiltration, carbon sequestration, and nutrient cycling, influencing the distribution and abundance of microbes, plants, and animals. [Martínez, et al. 2006](#) explores the role of biological soil crusts, demonstrating that crust formation by mosses and lichens depends on cover of bare soil and litter, soil respiration, potassium content, and aggregate stability. The fundamental role played by soil- and rock-community microbes, including desert biological soil crusts, in biogeochemical processes is further discussed in [Pointing and Belnap 2012](#) (cited under [Physiology and Genetics](#)). Similarly, [Ginzburg, et al. 2008](#) examines how soil-nesting activities of harvester ants influence pedologic properties and soil microbial diversity. Such bioturbation, as discussed in [Wilkinson, et al. 2009](#), is fundamental to understanding processes of soil formation, niche formation, and ecosystem evolution. The importance of edaphic features in maintaining regional soil biodiversity is further stressed in [Birkhofer, et al. 2012](#). The authors conclude that soil properties explain significant proportions of variation in fungal and soil fauna abundance and diversity, even after accounting for heterogeneity resulting from large-scale differences among sampling locations and land-use types. Similar influences of geopedaphic factors are noted in aboveground patterns of biodiversity. [Higgins, et al. 2011](#) demonstrates how geologic and edaphic features control floristic diversity within Amazonian forests, and that proper management requires a regional approach that takes geopedaphic-biotic affinities into consideration. [Zhang, et al. 2013](#) examines the relative importance of topography and edaphic

properties in the assembly of karst-adapted plant communities. The authors' work suggests that steepness of slope and depth of soil are critical factors in the formation of plant communities within karst forests. Further, historic geological events such as tectonics and orogenic activity greatly influence biogeography, ecology, and evolution. [Wright and Stigall 2013](#) uses phylogenetic biogeographic analyses to examine how historic geologic and oceanographic processes have influenced brachiopod speciation and patterns of dispersal. Additional references for biogeographic patterns that have resulted from vicariant events are cited under [Biogeography](#).

- Birkhofer, Klaus, Ingo Schöning, Fabian Alt, et al. 2012. General relationships between abiotic soil properties and soil biota across spatial scales and different land-use types. *PLoS ONE* 7.8: e43292.

The paper explores the relationships between soil properties and soil biota across large spatial scales and different land-use types spanning the latitudinal gradient of Germany. Abiotic soil properties explained significant amounts of variation in fungal, meso- and macrofauna, but not in yeast or bacterial biomass or diversity.

- Ginzburg, Orit, Walter G. Whitford, and Yosef Steinberger. 2008. Effects of harvester ant (*Messor* spp.) activity on soil properties and microbial communities in a Negev desert ecosystem. *Biology and Fertility of Soils* 45:165–173.

The study reports changes in soil microbial biomass and functional diversity resulting from harvester ant activity. Ant activity increased organic matter, soluble nitrogen, and microbial activity in nest-modified soils in comparison to control soils, suggesting that the effect of nests on soil fertility results from increased microbial biomass and activity.

- Higgins, Mark A., Kalle Ruokolainen, Hanna Tuomisto, et al. 2011. Geological control of floristic composition in Amazonian forests. *Journal of Biogeography* 38:2136–2149.

The study reports that Amazonian forests are partitioned into large-area units based on geologic and edaphic features, and the evolution of the units through geological time provides a mechanism for species diversification. Thus, it concludes that land use, management, and conservation approaches must be implemented on a regional basis.

- Martínez, Isabel, Adrián Escudero, Fernando T. Maestre, Azucena de la Cruz, César Guerrero, and Augustin Rubio. 2006. Small-scale patterns of abundance of mosses and lichens forming biological soil crusts in two semi-arid gypsum environments. *Australian Journal of Botany* 54:339–348.

The authors test whether the spatial patterning of lichens and mosses is related to surface and subsurface soil variables in two semiarid gypsum environments in Spain. Their results show that bare soil and litter cover, soil respiration, potassium content, and aggregate stability are drivers of biological soil crust composition and abundance.

- Wardle, David A. 2006. The influence of biotic interactions on soil biodiversity. *Ecology Letters* 9:870–886.

This review examines the biotic factors and mechanisms influencing soil community diversity across spatial scales. It concludes that a better understanding of biotic drivers of soil biodiversity are important to address topics in community and ecosystem ecology, such as aboveground-belowground interactions and the relationship between biodiversity and ecosystem functioning.

- Wilkinson, Marshall T., Paul J. Richards, and Geoff S. Humphreys. 2009. Breaking ground: Pedological, geological, and ecological implications of soil bioturbation. *Earth-Science Reviews* 97:257–272.

Bioturbation, resulting from the stirring and mixing of soil and sediments by organisms, is discussed as a fundamental process contributing to soil and landscape evolution, ecosystem engineering, niche construction, and carbon cycling.

- Wright, David F., and Alycia L. Stigall. 2013. Geologic drivers of late Ordovician faunal change in Laurentia: Investigating links between tectonics, speciation, and biotic invasions. *PLoS ONE* 8.7: e68353.

The paper investigates causal links between a dramatic turnover in orthid brachiopods and two dominant geologic processes, the Taconian Orogeny and Guttenberg carbon isotope excursion (GICE)-related global cooling, operating within Laurentia during the late Ordovician. Phylogenetic biogeographic analyses reveal how geologic and oceanographic processes have influenced brachiopod speciation and patterns of dispersal.

- Zhang, Zhong-hua, Gang Hu, and Jian Ni. 2013. Effects of topographical and edaphic factors on the distribution of plant communities in two subtropical karst forests, southwestern China. *Journal of Mountain Science* 10:95–104.

Study of relationships between topography and edaphic properties and the distribution of plant communities suggests that topographical factors are more important than edaphic factors in influencing local plant distribution on steep slopes with extensive rock outcrops, while edaphic factors are more influential on gentle slopes and relatively deep soils.

Biological Weathering

Mineral weathering of rocks and soils is an important process of nutrient element release in forms available for plant and microbial uptake. Mineral weathering is a pedological process responsible for the development of soils upon or within which many organisms live and, therefore, a fundamental aspect of geocology. Changes in the mode and rate of weathering can influence the type of soil that is produced and the ecology of the habitats overlying those soils. Organisms such as bacteria, fungi, lichens, plants, invertebrates, and other animals play a critical role in the weathering of rocks and soils, including in modifying the soil structure that impacts infiltration, drainage, aeration, pH, cation exchange capacity, and nutrient availability. Thus, any variation in biological weathering of minerals and the formation of soils can have a direct effect on ecology in both below- and aboveground habitats, and therefore can affect biodiversity.

[Abbott and Murphy 2007](#) is a good resource for an overview of the role fauna, flora, and microbes play in the chemical and physical weathering of minerals and the formation of soils. Plants play an important role in weathering via the mechanical/physical actions of their roots and by the chemicals they secrete into the rhizosphere for facilitating or restricting ion uptake, or for defensive (or allelopathic) purposes. [Lucas 2001](#) and [Andrews, et al. 2008](#) are two good sources to explore aspects of weathering and soil formation under the influence of plants. Microbial weathering has attracted much attention over the last several decades. [Uroz, et al. 2009](#) is a useful source for information on bacterial weathering, while [Hoffland, et al. 2004](#) explores the role of fungi in mineral weathering and pedogenesis. Plant-fungal-mineral interactions are the focus of a study, [Smits, et al. 2008](#), that shows the intricate and reciprocal relationships that ectomycorrhizal fungi have with plants (enabling them to be effective agents of mineral weathering). Lichen influences on mineral weathering have also been a focus of investigations in recent decades. [Chen, et al. 2000](#) is an early but comprehensive review of the processes of chemical and physical weathering of rocks by lichens. The study of biological weathering, especially by bacteria and fungi, also has wide-ranging applications in biotechnology. [Mapelli, et al. 2012](#) is an excellent source for a discussion on how findings from microbe-substrate weathering studies can contribute to the fields of agriculture, bioremediation, and other bioremediation and environmental technologies.

- Abbott, Lynette K., and Daniel V. Murphy, eds. 2007. *Soil biological fertility: A key to sustainable land use in agriculture*. Dordrecht, The Netherlands: Springer.

The volume consists of twelve chapters on biological aspects of soil fertility, including the role animals, plants, fungi, and other microorganisms play in the chemical and physical transformation of soil. While the focus is on soil fertility for agricultural purposes, the information is pertinent to other topics in geocology.

- Andrews, Megan Y., Jay J. Ague, and Robert A. Berner. 2008. Weathering of soil minerals by angiosperm and gymnosperm trees. *Mineralogical Magazine* 72:11–14.

The paper examines quantitative weathering rates of angiosperms and gymnosperms by investigating their plant-mineral interactions in a temperate field setting underlain by granodiorite. The observed root-mineral interactions suggest slightly more weathering of Ca-bearing minerals by the angiosperms, and significantly more weathering of the Mg-bearing minerals by the gymnosperms.

- Chen, Jie, Hans-Peter Blume, and Lothar Beyer. 2000. Weathering of rocks induced by lichen colonization: A review. *Catena* 39:121–146.

The review discusses the role lichens play in the weathering of rock and other mineral substrates. Physically induced weathering—caused by mechanical disruption of rocks by hyphal penetration and expansion, and by contraction of lichen thalli and chemically induced weathering via the excretion of various organic acids (particularly oxalic acid)—is highlighted.

- Hoffland, Ellis, Thomas W. Kuyper, Håkan Wallander, et al. 2004. The role of fungi in weathering. *Frontiers in Ecology and the Environment* 2:258–264.

The review is an excellent source of information on the taxonomy and ecology of fungi responsible for biological weathering and the physical and chemical means by which fungi weather rocks. Areas of future research on fungal-mineral interactions are also highlighted.

- Lucas, Yves. 2001. The role of plants in controlling rates and products of weathering: Importance of biological pumping. *Annual Review of Earth and Planetary Sciences* 29:135–163.

The critical role plants play in controlling the rates and products of weathering is the topic of this review. The influences of plants in controlling water dynamics, mechanical weathering, and the chemistry of weathering solutions are highlighted.

- Mapelli, Francesca, Ramona Marasco, Annalisa Balloi, et al. 2012. Mineral–microbe interactions: Biotechnological potential of bioweathering. *Journal of Biotechnology* 157:473–481.

The roles of bacteria and fungi in mineral dissolution are discussed in relation to their biotechnological potential, including in increasing crop productivity in arid lands, bioremediation, and other bioremediation and environmental technologies.

- Smits, Mark M., Steeve Bonneville, Simon Haward, and Jonathan R. Leake. 2008. Ectomycorrhizal weathering, a matter of scale? *Mineralogical Magazine* 72:131–134.

The paper investigates plant-fungal-mineral interactions, showing that ectomycorrhizal fungi are actively engaged in the weathering of apatite and biotite, and that carbon from a tree is actively transported to the fungus where it is preferentially allocated to areas with minerals containing weatherable supplies of essential nutrients.

- Uroz, Stéphane, Christophe Calvaruso, Marie-Pierre Turpault, and Pascale Frey-Klett. 2009. Mineral weathering by bacteria: Ecology, actors and mechanisms. *Trends in Microbiology* 17:378–387.

The paper discusses the ecological relevance of bacterial weathering and highlights molecular mechanisms and genetic determinants involved in the dissolution of complex minerals under aerobic conditions, and potential applications of genomic resources to the study of bacterial weathering.

Extremophiles

Extremophiles are organisms able to thrive under conditions inhospitable for most other biota. While there is much attention on microbes as model organisms for the study of extremophile ecology, physiology, genetics, and evolution, the study of plants and animals of extreme

geoedaphic settings, such as alkaline, acidic, hypersaline, and metal-enriched substrates, has also generated much interest in recent years. [Bell 2012](#) and [Rampelotto 2013](#) are comprehensive treatments containing original research and review papers on plants, animals, and microbes found in extreme settings, including those that have arisen from geologic or edaphic phenomena. Plant-specific literature deals with adaptations to chemically extreme substrates such as serpentinites as illustrated in [Brady, et al. 2005](#) (cited under [Evolutionary Aspects](#)), and to gypsum and dolomite as discussed in [Escudero, et al. 2014](#) and [Pignatti and Pignatti 2014](#) (cited under [Flora](#)), respectively. [Jenks and Hasegawa 2014](#) (cited under [Physiology and Genetics](#)) reports on early-21st-century discoveries of adaptations to common geoedaphic stresses encountered by plants, including salinity, heavy metals, drought, and flooding. There is extensive literature summarizing microbial extremophiles in terrestrial and aquatic landscapes. [Seckbach 2007](#) (cited under [Bacteria, Protists, Fungi, and Lichens](#)) is an excellent source for information on the diversity, ecology, and physiology of algae and cyanobacteria tolerant of extreme environments. [Margesin and Miteva 2011](#) reviews microbe adaptations to cold environments, while [Cardace and Hoehler 2011](#); [McCollom and Seewald 2013](#); and [Takai, et al. 2005](#) discuss microbial evolution in, and tolerance to, serpentinite habitats. As the serpentinitization process creates highly reducing conditions, producing hydrogen and methane for metabolic energy, serpentinites are a prime target for the study of early life. [Pikuta, et al. 2007](#), while providing a good general overview of microbial tolerances to various extreme environments, highlights advances in the study of microfossils in meteorites and the significance of microbial extremophiles to the study of astrobiology. [Gerday and Glansdorff 2007](#) provides a comprehensive review of the biochemical and physiological bases for tolerance among thermophiles, psychrophiles, halophiles, acidophiles, piezophiles, and alkaliphiles, and discusses biotechnological applications of extremophiles.

- Bell, Eleanor. 2012. *Life at extremes: Environments, organisms, and strategies for survival*. Oxford: CABI.

This authoritative treatment describes the biological, ecological, and biogeochemical challenges faced by microbes, plants, and animals living in harsh environments worldwide, including polar environments and hot deserts; acidic, alkaline, and hypersaline flats; caves and karst settings; and terrestrial and deep sea hydrothermal vents.

- Cardace, Dawn, and Tori M. Hoehler. 2011. Microbes in extreme environments: Implications for life on the early Earth and other planets. In *Serpentine: The evolution and ecology of a model system*. Edited by Susan P. Harrison and Nishanta Rajakaruna, 29–48. Berkeley: Univ. of California Press.

This chapter discusses how serpentinitizing systems serve as habitat for extremophile microbes (those inhabiting the high-pH, Ca²⁺-rich waters circulating in serpentinite bodies) and how they provide novel ground for scientific investigation into extremophile evolution and life on other planets.

- Gerday, Charles, and Nicolas Glansdorff, eds. 2007. *Physiology and biochemistry of extremophiles*. Washington, DC: ASM.

The book provides a comprehensive review of the physiological ecology, biochemistry, evolutionary aspects, and biotechnological applications of all known types of extremophiles, including thermophiles, psychrophiles, halophiles, acidophiles, piezophiles, and alkaliphiles.

- Margesin, Rosa, and Vanya Miteva. 2011. Diversity and ecology of psychrophilic microorganisms. *Research in Microbiology* 162:346–361.

The review focuses on the abundance, taxonomic, and functional biodiversity; low temperature adaptation; and biogeography of microbial communities belonging to *Bacteria*, *Archaea*, and *Eukarya* from a range of aquatic and terrestrial cold environments.

- McCollom, Thomas M., and Jeffrey S. Seewald. 2013. Serpentinites, hydrogen, and life. *Elements* 9.2: 129–134.

The paper describes how serpentinization creates highly reducing conditions, producing hydrogen and methane that can then be used by some microorganisms for generating metabolic energy and biomass, making serpentinites a major focus in the study of the origin of life on Earth and elsewhere in our solar system.

- Pikuta, Elena V., Richard B. Hoover, and Jane Tang. 2007. Microbial extremophiles at the limits of life. *Critical Reviews in Microbiology* 33:183–209.

The review discusses the status to date in all fields of extremophiles and summarizes the limits of life for different species of microbial extremophiles. Early-21st-century studies of microfossils in meteorites are also highlighted to discuss the significance of microbial extremophiles to astrobiology.

- Rampelotto, Pabulo H., ed. 2013. *Special issue: Extremophiles and extreme environments*. *Life* 3:1–517.

The volume devotes three issues to the discussion of wide-ranging topics relating to microbial and other extremophiles inhabiting terrestrial and aquatic habitats. The papers in this volume focus on extremophile diversity, ecology, physiology, genetics, and evolution. Available [online](#).

- Takai, Ken, Craig L. Moyer, Masayuki Miyazaki, et al. 2005. *Marinobacter alkaliphilus* sp. nov., a novel alkaliphilic bacterium isolated from subseafloor alkaline serpentine mud from Ocean Drilling Program Site 1200 at South Chamorro Seamount, Mariana Forearc. *Extremophiles* 9.1: 17–27.

Physiological and molecular approaches are used to identify a new bacterium species isolated from a sub-seafloor serpentinite mud volcano, illustrating the potential of serpentinite sites to harbor undescribed species.

Bacteria, Protists, Fungi, and Lichens

Terricolous (soil dwelling) and saxicolous (rock dwelling) microorganisms and lichens play a fundamental role in the ecology of both below- and aboveground habitats via their influence on biogeochemical processes, including weathering, pedogenesis, nutrient cycling, and nutrient acquisition by plants. Thus, much attention has been paid to characterize the biodiversity of such organisms, including the important role they play in biogeochemical processes. [Kirchman 2012](#) is an excellent resource for information on microbial geocology and biogeochemistry.

Microorganisms and lichens associated with unusual and often-extreme geodaphic settings have been a focus of many investigations, primarily due to their unique physiological and biochemical adaptations to their chemically and physically harsh substrate. [Beyer and Bölter 2002](#) examines the ecology of microbes and other biota found in ice-free Antarctic landscapes. The chapter on heterotrophic microbes and their microbial and enzymatic activities is especially relevant to microbial geocology. Ultramafic (iron- and magnesium-rich) rocks have also been a focus of geocological study (see [Brady, et al. 2005](#) and [Harrison and Rajakaruna 2011](#), both cited under [Evolutionary Aspects](#)) due to the unusual soils they generate and the unique biota they harbor. [Southworth, et al. 2014](#) reviews ectomycorrhizal and arbuscular mycorrhizal symbioses on and off ultramafic soils. [Rajakaruna, et al. 2012](#) examines lichens of ultramafic and nonultramafic rocks in California and concludes that the lichens often differ between rock types, and that species richness is greater on ultramafic rocks. The authors suggest that a combination of chemical and physical attributes of the rocks may drive the diversity of saxicolous lichens. The microbial ecology of heavy metal-rich soils is also a major focus due to its biotechnological and bioremediation potential. [Giller, et al. 2009](#) is a good resource on this topic. Salinity is another stressor impacting soils worldwide. [Casamayor, et al. 2013](#) demonstrates the use of modern genetic tools to characterize microbial diversity of saline lakes. The role that land-use history can play in bacterial diversity is the focus of the study in [Guan, et al. 2013](#). The authors conclude that the bacterial communities are influenced by both geochemical factors and land-use practices, and that agricultural lands harbor more homogenized communities compared to those in pristine settings. While aspects of bacterial and fungal geocology have received much attention, the literature on protists and other eukaryotic microbes is limited. [Seckbach 2007](#), however, is a good resource for studies on the diversity, ecology, and physiology of stress-tolerant algae and cyanobacteria. [Bell 2012](#) and [Rampelotto 2013](#) (both cited under [Extremophiles](#)) also contain useful information regarding the diversity and geocology of microbes.

- Beyer, Lothar, and Manfred Bölter, eds. 2002. *Geocology of Antarctic ice-free coastal landscapes*. Ecological Studies 154. Berlin: Springer.

This volume describes typical terrestrial environments of the maritime and continental Antarctic, focusing on interactions among soils, microbes, plants, and animals. One chapter is devoted to the discussion of heterotrophic microbes and their microbial and enzymatic activities in Antarctic soils.

- Casamayor, Emilio O., Xavier Triadó-Margarit, and Carmen Castañeda. 2013. Microbial biodiversity in saline shallow lakes of the Monegros Desert, Spain. *FEMS Microbiology Ecology* 85:503–518.

The paper reports the findings from a rRNA gene fingerprinting and sequencing study of the diversity of bacteria, archaea, and microbial eukaryotes from saline lakes with large salinity (2.7–22.1 percent) and temperature ranges (1.5–35.3°C). The groups exhibited differential tolerances to the abiotic stresses and often dominated distinct habitats.

- Giller, Ken E., Ernst Witter, and Steve P. McGrath. 2009. Heavy metals and soil microbes. *Soil Biology and Biochemistry* 41:2031–2037.

Advances in the ecotoxicological assessment of heavy metals and their effects on soil organisms are the focus of this review. The need for long-term experiments and basic research on how microorganisms are exposed to and respond to metals in soils is also emphasized.

- Guan, Xiangyu, Jinfeng Wang, Hui Zhao, et al. 2013. Soil bacterial communities shaped by geochemical factors and land use in a less-explored area, Tibetan Plateau. *BMC Genomics* 14:820–833.

The study shows that the bacterial community structure and functions are influenced by both human activities and soil environmental properties, and that the bacterial communities appeared to be more homogenized in farmland soils compared to pristine alpine meadows. Available [online](#).

- Kirchman, David L. 2012. *Processes in microbial ecology*. New York: Oxford Univ. Press.

The fourteen chapters are an excellent introduction to the ecology of viruses, bacteria, fungi, protozoa, and other protists in freshwater, marine, and terrestrial ecosystems. The primary focus of the book is microbial influences on biogeochemical processes.

- Rajakaruna, Nishanta, Kerry Knudsen, Alan M. Fryday, et al. 2012. Investigation of the importance of rock chemistry for saxicolous lichen communities of the New Idria serpentinite mass, San Benito County, California, USA. *Lichenologist* 44.5: 695–714.

This is one of only a handful of comparative studies of lichens of serpentinite and nonserpentinite rocks in North America. Lichen assemblages between the two rock types were significantly different at the species level but not at the generic level, with species richness significantly greater on the serpentinite rocks.

- Seckbach, Joseph, ed. 2007. *Algae and cyanobacteria in extreme environments*. Cellular Origin, Life in Extreme Habitats and Astrobiology 11. Dordrecht, The Netherlands: Springer.

The edited volume provides an overview of protists that dominate extreme environments, including those resulting from geodaphic processes. The diversity, ecology, physiology, and evolution of species found under extreme levels of temperature, pH, salt

concentrations, UV radiation, moisture, heavy metals, anaerobic conditions, illumination, and hydrostatic pressure are discussed.

- Southworth, Darlene, Linda E. Tackaberry, and Hugues B. Massicotte. 2014. Mycorrhizal ecology on serpentine soils. *Plant Ecology and Diversity* 7.3: 445–455.

This review asks whether the diversity of plants on serpentinite-derived soils correlates with that of mycorrhizal fungi. Plants formed abundant ectomycorrhizal and arbuscular mycorrhizal symbioses both on and off of serpentinite. Ectomycorrhizal fungal communities did not differ between soil types, but arbuscular mycorrhizal communities differed in some cases and not others.

Flora

The geocology of plants has been a primary focus of studies in natural history, biogeochemistry, ecology, evolution, conservation biology, and the agricultural sciences. The intimate and inseparable relationship between plants and their substrate results from the need for plants to obtain water and nutrients from the substrate upon which they grow. Thus, it is no surprise that chemical and physical attributes of the substrate control many aspects of plant ecology and evolution. Throughout history, plants closely associated with specific geologies have been described as indicators of minerals and elements found within them, and close observation of such substrate-plant relations has led to biogeochemical prospecting worldwide. [Brooks 1983](#) and [Martin and Coughtrey 1982](#) (cited under [General Overviews](#)) are excellent resources for the early literature on plants adapted to heavy metal and other mineral-rich geologies. Current geocological treatments are primarily involved in describing unique floras associated with chemically and physically harsh geodaphic conditions. In this regard, much attention has been paid to endemic- and rare plant-rich communities of serpentinite rocks. [Brooks 1987](#) and [Roberts and Proctor 1992](#) (cited under [General Overviews](#)) are excellent early resources for serpentinite-associated floras. More recent treatments include [Kruckeberg 2002](#) and [Alexander, et al. 2007](#) (both cited under [General Overviews](#)), along with [Brady, et al. 2005](#) and [Harrison and Rajakaruna 2011](#) (both cited under [Evolutionary Aspects](#)). Calcium-rich, alkaline geodaphic settings also contribute to distinct floras with high percentages of rare and endemic species. [Escudero, et al. 2014](#) is an up-to-date treatment on gypsum- (calcium sulfate) adapted plants, while [Pignatti and Pignatti 2014](#) covers dolomite- (calcium magnesium carbonate) associated floras of Europe. Plants associated with unique geomorphological features (mountains, deserts, peatlands, etc.) have also been of interest due to the unique adaptations they possess to tolerate climatic and other abiotic and biotic stressors. [Körner 2003](#) is a comprehensive treatment of the physiological ecology and evolution of plants in alpine environments. [Ward 2009](#) is an outstanding resource for plant adaptations to desert environments, while [Rydin and Jeglum 2006](#) is an authoritative treatment of plants in peatlands. The latter three references also deal with climate change-associated stressors influencing these unique plant communities, providing insight on how best to approach their management, conservation, and restoration. [Anderson, et al. 1999](#), although a little outdated, is a broad overview of the floristics, ecology, and conservation of specialized plant communities of edaphic islands and other unusual geocological settings in North America.

- Anderson, Roger C., James S. Fralish, and Jerry M. Baskin, eds. 1999. *Savannas, barrens, and rock outcrop plant communities of North America*. Cambridge, UK: Cambridge Univ. Press.

The twenty-six chapters discuss climate, geology, soils, and historic and current vegetation of plant communities of savannas, woodlands, barrens, and rock outcrops throughout the United States and Canada. The book provides an excellent overview of North America's edaphic islands and their unique vegetation, including their conservation, restoration, and management.

- Brooks, Robert R. 1983. *Biological methods of prospecting for minerals*. New York: John Wiley.

A useful resource listing plant and animal species associated with metal-enriched geologies worldwide. Chapter discussions include the history of geobotany in mineral exploration, plant communities used as indicators of mineralization, and plant species effective for indicating a range of widespread heavy metals.

- Brooks, Robert R. 1987. *Serpentine and its vegetation: A multidisciplinary approach*. Ecology, Phytogeography and Physiology 1. Portland, OR: Dioscorides.

An early overview of serpentine geocology, this volume provides a summary of research on serpentinite habitats worldwide, including information on soils, plants, animals, and agriculture.

- Escudero, Adrián, Sara Palacio, Fernando Maestre, and Arantzazu Luzuriaga. 2014. Plant life on gypsum: A review of its multiple facets. *Biological Reviews*.

All aspects of plant life on gypsum, from species to ecosystem levels, are discussed along with the processes related to the structure of gypsum plant communities. Research on the ecology and evolution of gypsum plants is highlighted and putative mechanisms to tolerate and adapt to gypsum soils are summarized.

- Körner, Christian. 2003. *Alpine plant life: Functional plant ecology of high mountain ecosystems*. 2d ed. Heidelberg, Germany: Springer.

The book covers a wide range of topics of alpine environments worldwide, including climate and substrate, floristics and phytogeography, physiological ecology, and anthropogenic impacts on alpine vegetation.

- Pignatti, Erika, and Sandro Pignatti. 2014. *Plant life of the dolomites: Vegetation structure and ecology*. New York: Springer.

Using the authors' extensive combined research, the book explores biological, geological, climatic, and physiochemical parameters of dolomite-associated plant communities in

Europe, including their floristic composition, indicator taxa, habitat alteration risks, and conservation value.

- Rydin, Hakan, and John K. Jeglum. 2006. *The biology of peatlands*. New York: Oxford Univ. Press.

The book provides an overview of the ecology of peatlands (marsh, swamp, fen, and bog) and the adaptations of plants and other biota to moss-dominated permanent wetlands. Management, conservation, and restoration of peatlands are also discussed along with the influences of climate change on their biota.

- Ward, David. 2009. *The biology of deserts*. New York: Oxford Univ. Press.

The eleven chapters in this comprehensive treatment on the biology, ecology, and evolution of desert plants and animals covers wide-ranging topics associated with this arid and resource-poor ecosystem, including stressors impacting desert plants worldwide. It also emphasizes applied issues such as desertification and invasive species, and desert conservation.

Fauna

Since plants are a major component of the habitat of animals, geology often affects faunas indirectly through its effects on vegetation or climate. Direct effects are more subtle, but occur in many ways. Some geological substrates, such as limestone, are especially prone to the formation of caves, and these subterranean habitats have fascinating specialized and unique faunas: [Lin and Li 2014](#) (cited under [Conservation](#)) describes five new spider species from caves in China. [Culver and Pipan 2009](#) provides an excellent general overview of cave environments and the biological processes that generate and sustain their biota. Some geological materials produce substrates with colors (black, white, red, etc.) that are important habitat components for animals. Substrate color affects soil temperature: [Hadley, et al. 1992](#) illustrates how black volcanic sand versus white sand beaches influences the ecology and behavior of tiger beetles in New Zealand. Substrate color also influences the visibility of animals to predators, and there are many examples of animal color evolving to match that of the substrate. [Linnen, et al. 2013](#) provides an example by investigating the evolution of the light coat color in deer mice from light-colored soils in the Nebraska Sandhills, United States. Another habitat feature influenced by geology is soil texture: this can directly influence the ability of animals to burrow or affect the structural integrity of burrows. [M'Rabet, et al. 2007](#) describes the importance of soil texture to burrow construction of an endangered spider. It also should be recognized that animals can affect landscapes, and the importance and extent of their effects can differ depending on geology. [Butler 1995](#) provides a good overview of animal impacts on landscapes and the associated literature prior to that date. The fauna of island habitats (both oceanic and edaphic) has received much study (see section on [Biogeography](#)): Foster's Rule, which contends that many island faunas evolve smaller (dwarfism) or larger (gigantism) sizes than mainland animals, is a fascinating example. [Case 1978](#) is a classic paper that helped establish Foster's Rule and stimulate its continuing investigation by biogeographers in the early 21st century. Other island biogeography concepts are often applicable to faunas restricted to unique geological areas. As an

example, [Michael, et al. 2008](#) studied the reptile fauna of granite outcrops in southeastern Australia, finding that many factors (patch size, matrix condition, habitat structure, etc.) affected reptile diversity.

- Butler, David R. 1995. *Zoogeomorphology: Animals as geomorphic agents*. New York: Cambridge Univ. Press.

Good overview of how animal activities (burrowing, trampling, soil ingestion, etc.) change landscape features (by erosion and transport/deposition of sediment) and thus are a powerful ecological force. Terrestrial animals (including invertebrates) are emphasized, but aquatic animals are also included.

- Case, Ted. 1978. A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* 59:1–18.

The author expands on Foster's initial work to explore both island gigantism and dwarfism, setting the theoretical stage for later biogeographers. Foster's Rule continues to stimulate research, and its tenets are debated in the ecological and evolutionary literature.

- Culver, David, and Tanja Pipan. 2009. *The biology of caves and other subterranean habitats*. New York: Oxford Univ. Press.

A good introduction to the fauna of caves and related scientific literature. The book focuses on important biological topics including adaptation, speciation, community ecology, and conservation of cave biota.

- Hadley, Neil F., Anthony Savill, and Thomas D. Schulz. 1992. Coloration and its thermal consequences in the New Zealand tiger beetle *Neocicindela perhispidata*. *Journal of Thermal Biology* 17:55–61.

This paper is an excellent example of how substrate color (beaches made of either black or white sand) influences its temperature and how the behavior of an insect species occupying these habitats is modified in response.

- Linnen, Catherine, Yu-Ping Poh, Brant Peterson, et al. 2013. Adaptive evolution of multiple traits through multiple mutations at a single gene. *Science* 339:1312–1316.

Finding greater predation risk for mice whose coat color does not match soil color, the authors explore the origins of light coat color found in mice on sandy soils. They discovered that multiple mutations in a single gene have independently resulted in the adaptive light coloration of these mice.

- Michael, Damlan, Ross Cunningham, and David Lindenmayer. 2008. A forgotten habitat? Granite inselbergs conserve reptile diversity in fragmented agricultural landscapes. *Journal of Applied Ecology* 45:1742–1752.

Applying island biogeography concepts to granite outcrops, the authors generally find results congruent with theory. They conclude that reptile conservation is maximized when features of both the outcrop and the surrounding habitat matrix can be manipulated to favor reptile persistence.

- M'Rabet, Salima Machkour, Yann Hénaut, Alejandra Sepúlveda, Roberto Rojo, Sophie Calmé, and Violette Geissen. 2007. Soil preference and burrow structure of an endangered tarantula, *Brachypelma vagans* (Mygalomorphae: Theraphosidae). *Journal of Natural History* 41:1025–1033.

This study revealed that soil features were important to burrow construction, and that clay soils were preferred over sandy soils or soils with large amounts of roots. This information can help managers interested in conserving this rare species in remaining populations or reintroducing it at other sites.

Biogeography

Geology is one of many factors that influence the distribution of organisms across Earth's surface. Organisms are usually distributed in a patchy manner, and geology is an important habitat feature that often contributes to patchiness. [Cox and Moore 2010](#) provides an excellent overview of the general field of biogeography, including both classic and more recent literature. Patchy habitats can be terrestrial islands in an aquatic matrix (e.g., oceanic islands), and classical Island Biogeography Theory was first developed for these situations. [Whittaker and Fernández-Palacios 2007](#) is a good introduction to island biogeography, including the history of the field. [Bramwell and Caujape-Castells 2011](#) provides an exploration of the biology and ecology of island floras, including ecological and evolutionary perspectives as well as important conservation implications. Islands can also be edaphic, when geological differences give rise to habitats that form patches within a matrix of very different soils. There has been much interest in applying Island Biogeography Theory to these edaphic islands, and in general the theory's predictions have been found to hold. [Schenk 2013](#) tests the prediction that dispersal ability in the plant genus *Mentzelia* should evolve to limit dispersal in species endemic to patches of gypsum soils. As theory predicts, the researcher finds that seeds of edaphic endemics of this wind-dispersed plant genus have smaller wings and thus have restricted dispersal abilities. Edaphic factors are an important contributor to plant speciation (see section on [Evolutionary Aspects](#)). [Fine, et al. 2013](#) explores edaphic specialist and generalist tree species in the most species-rich habitat on Earth, lowland tropical rainforest, concluding that edaphic variability is an important factor promoting genetic differentiation in tropical tree species. The importance of soil diversity to biological diversity is recognized by the concept of soil endemism. The exploration in [Bockheim and Schliemann 2014](#) of the contribution of soil endemism to plant endemism in Wisconsin, United States, showed a weak correlation. High mountains also contribute to unique patterns of biodiversity, and [Nagy and Grabherr 2009](#) and [Körner 2003](#) (cited under [Flora](#)) provide excellent overviews of the biogeography of alpine environments. Finally, there are important applications of biogeography for conservation. [Ladle and Whittaker 2011](#) provides a good introduction to these applications, which are further explored in the section on [Conservation](#).

- Bockheim, James G., and Sarah A. Schliemann. 2014. Soil richness and endemism across an environmental transition zone in Wisconsin, USA. *Catena* 113:86–94.

Testing the concept that soil endemism should be positively correlated with plant endemism, the authors examine soil and plant distributions across a transition zone. They find that plant endemism correlated more closely with landform than to soil taxa, but still report important associations between geological substrate and plant species distributions.

- Bramwell, David, and Juli Caujape-Castells. 2011. *The biology of island floras*. Cambridge, UK: Cambridge Univ. Press.

This edited volume contains twenty-one chapters covering a wide range of topics focused on island plant communities. Some chapters focus on specific islands, whereas others deal more broadly with topics such as reproductive biology, ecology, invasive species, conservation, climate change, etc.

- Cox, C. Barry, and Peter D. Moore. 2010. *Biogeography: An ecological and evolutionary approach*. 8th ed. Hoboken, NJ: John Wiley.

A broad overview of the field of biogeography, this book is a good introduction to the principles of the field and its underlying literature.

- Fine, Paul, Felipe Zapata, Douglas Daly, et al. 2013. The importance of environmental heterogeneity and spatial distance in generating phylogenetic structure in edaphic specialist and generalist tree species of *Protium* (Burseraceae) across the Amazon basin. *Journal of Biogeography* 40:646–661.

The authors build on prior work done in this rainforest system that contains edaphic specialist and generalist species. After examining the genetic structuring of two species, they conclude that edaphic heterogeneity is an important mechanism promoting genetic differentiation on this habitat type.

- Ladle, Richard, and Robert Whittaker. 2011. *Conservation biogeography*. Hoboken, NJ: Wiley-Blackwell.

This edited volume examines connections between biogeography and conservation biology, suggesting that conservation biogeography is emerging as a new subdiscipline of conservation biology. It explores how understanding biodiversity patterns can inform conservation planning and better preserve Earth's biota.

- Nagy, Laszlo, and Georg Grabherr. 2009. *The biology of Alpine habitats*. New York: Oxford Univ. Press.

The authors provide a global overview of alpine habitats and the biota they harbor, including the abiotic and biotic factors that have shaped these island-like and biodiverse habitats over ecological and evolutionary timescales.

- Schenk, John. 2013. Evolution of limited seed dispersal ability on gypsum islands. *American Journal of Botany* 100:1811–1822.

Oceanic island species often have limited dispersal ability since those islands are surrounded by unsuitable habitat into which dispersal wastes potential offspring. The author finds *Mentzelia* species endemic to gypsum soil islands have evolved relatively small-winged seeds, thus limiting their dispersal into adjacent habitats in which they are poor competitors.

- Whittaker, Robert J., and José María Fernández-Palacios. 2007. *Island biogeography: Ecology, evolution, and conservation*. 2d ed. Oxford: Oxford Univ. Press.

This book builds on the classic studies of island biogeography to show how islands have been used as model systems for studies of evolution, community ecology, etc. The book also describes island formation and environmental development to tie island geology into island biology.

Ecological Aspects

Geology and ecology are tightly linked in many cases and by many processes: [Huggett 1995](#) (cited under [General Overviews](#)) provides an excellent introduction. Climate exerts a major influence on the mineral weathering of geological substrates as well as on the composition of biological communities, and within a climate zone geological substrate often drives community characteristics. [Hahm, et al. 2013](#) provides an illustration of this principle: within a climatic zone the local composition of granite influenced vegetation, and that (by influencing erosion rates) controlled landform formation. On a large scale, geology determines climate: position on the planet (especially latitude) is important; but also, mountains change climate through effects of elevation on temperature and rainfall. In addition, the orientation (aspect) and steepness of the surface (slope) also affect microclimates. These microclimate effects are themselves magnified as latitude increases. [Warren 2010](#) tested the relationship between aspect and microclimate variation in temperate forest herbs. The author found that the abiotic features that explained species' responses to aspect varied between the species used, showing that underlying ecological explanations for aspect responses are not universal across species. Geology influences topographic variation because different materials erode at different rates, creating landscape complexity with important effects on biological communities. As a type of rapid erosion, for example, landslides can be important geological and ecological factors in landscapes: [Walker and Shiels 2013](#) provides an excellent overview. Other geological events (such as volcanoes) also have dramatic effects on biota: [Dale, et al. 2005](#) provides a wealth of information on how the eruption of Mount St. Helens in 1980 (Oregon, United States) affected biological communities and ecosystems, as well as on how they have recovered during the intervening years. All the above factors contribute to habitat diversity and, thus, are drivers of biological diversity. [Hortal, et al. 2009](#) provides an entry point into the literature regarding links between habitat diversity and biological diversity. Geological factors also affect community productivity by influencing availability of nutrients to primary producers. [Geider, et al. 2001](#) provides a broad overview of primary productivity on Earth and its limiting factors, including nutrient supply. Geological features serve as important pools of nutrients in most nutrient cycles in ecosystems.

The classic work [Vitousek 2004](#) (Hawaii, United States) illustrates connections between geological substrate and time that affect the nitrogen cycle and, through those connections, biological community function and composition. In this article, the [Biogeography](#) section explores how the spatial patterning of habitats (greatly affected by geological factors) influences biodiversity patterns, while other sections (including those on specific biological groups, e.g., [Fauna](#), etc.) provide other connections between geology and ecological topics.

- Dale, Virginia H., Frederick J. Swanson, and Charles M. Crisafulli, eds. 2005. *Ecological responses to the 1980 eruption of Mount St. Helens*. New York: Springer.

The twenty chapters in this edited volume provide a fascinating case study of the ecological effects of a famous 1980s volcanic eruption. Chapters cover responses of plant and animal communities, as well as effects on ecosystem processes.

- Geider, Richard, Evan deLucia, Paul Falkowski, et al. 2001. Primary productivity of planet earth: Biological determinants and physical constraints in terrestrial and aquatic habitats. *Global Change Biology* 7:849–882.

This broad consideration of primary production, its measurement, and its constraints in major global habitats provides context for the role of nutrient limitations in affecting this fundamental ecological process. The article also connects this topic to climate change and its potential ecological impacts.

- Hahm, W. Jesse, Clifford Riebe, Claire Lukens, and Sayaka Araki. 2013. Bedrock composition regulates mountain ecosystems and landscape evolution. *Proceedings of the National Academy of Sciences of the United States of America*.

The composition of granitic substrates in the Sierra Nevada of California, United States, is shown to be an important driver of ecosystem traits. By controlling vegetation type, substrate influences erosion rates and therefore development of landform features.

- Hortal, Joaquín, Kostas Triantis, Shai Meiri, Elisa Thébault, and Spyros Sfenthourakis. 2009. Island species richness increases with habitat diversity. *American Naturalist* 174:E205–E217.

In this review of the well-established positive relationship between habitat diversity and species richness, the authors examine the exact shape of the relationship and relate habitat diversity/species richness relationships to theoretical models of niche breadth.

- Vitousek, Peter. 2004. *Nutrient cycling and limitation: Hawai'i as a model system*. Princeton, NJ: Princeton Univ. Press.

Summarizing two decades of research, this award-winning book illustrates the importance of nutrient cycles to biological communities, including how time since island formation affects nutrient cycles, and through them, community composition.

- Walker, Lawrence, and Aaron Shiels. 2013. *Landslide ecology*. Cambridge, UK: Cambridge Univ. Press.

An excellent entry point into the literature on landslides, including connections between geological and biological phenomena as well as the impacts of landslides on human activities (and vice versa). The authors summarize landslide impacts on a wide range of organisms as well as impacts on ecological processes.

- Warren, Robert. 2010. An experimental test of well-described vegetation patterns across slope aspects using woodland herb transplants and manipulated abiotic drivers. *New Phytologist* 185:1038–1049.

After describing how aspect became recognized as an important ecological factor, the author investigates the abiotic factors responsible for aspect effects. He finds that the abiotic explanation depends on both species and its growth stage, and concludes that generalizations about abiotic drivers of aspect effects are difficult to make.

Evolutionary Aspects

Within a given climatic region, geological differences play a fundamental role in generating habitat heterogeneity, resulting in local adaptation and population differentiation leading to plant speciation. [Kruckeberg 1986](#) and [Rajakaruna 2004](#) explore the modes and mechanisms of speciation under the geodaphic influence using model plants from western North America. The study of ecological speciation, including that stemming from geodaphic influences, has long interested plant ecologists. [Turesson 1922](#) and [Clausen, et al. 1940](#) are two 20th-century classics of evolutionary ecology, describing how experimental methods such as common garden and reciprocal transplant studies can be used to examine the roles played by phenotypic plasticity and local adaptation in habitat specialization. Plants endemic to serpentinite-derived substrates have been effective models for the study of edaphically driven speciation. Several chapters in [Harrison and Rajakaruna 2011](#) explore key topics in the evolutionary process, including intraspecific variation, local adaptation, and modes of speciation using plants adapted to serpentinites of California. Additional chapters examine genomic and phylogenetic approaches to the study of plant speciation under the geodaphic influence. Although restricted to serpentinite-plant associations, [Brady, et al. 2005](#) is another excellent resource for evolutionary topics relating to substrate endemism. The roles that extreme habitats—such as oceanic pillow lavas, evaporitic settings, microbialites, stromatolites, and other deep subsurface and seafloor environments—play in the evolution of microbial life also have attracted much attention in the early 21st century. [Dilek, et al. 2008](#) is a useful resource for the study of extremophilic microbes in extreme geochemical settings. Macroevolutionary aspects of life through time, particularly of animal species, are often interpreted using the fossil record. [Patzkowsky and Holland 2012](#) is an authoritative treatment of how the distribution of fossil taxa in time and space is controlled not only by processes of ecology, evolution, and environmental change, but also by the stratigraphic processes that govern when and where fossil-containing sediment is deposited and preserved. For a broad overview of geodaphic influences on the ecology and evolution of plant and animal species and the assembly of their communities, see [Huggett 1995](#) (cited under [General Overviews](#)).

- Brady, Kristy U., Arthur R. Kruckeberg, and Harvey D. Bradshaw Jr. 2005. Evolutionary ecology of plant adaptation to serpentine soils. *Annual Review of Ecology, Evolution, and Systematics* 36:243–266.

This review covers the defining features of serpentinite-derived soils and the mechanisms proposed for serpentinite tolerance. It also addresses the evolution and genetics of serpentinite adaptation and how speciation may occur under its influence.

- Clausen, Jens C., David D. Keck, and William M. Hiesey. 1940. *Experimental studies on the nature of species*. Vol. 1, *Effects of varied environments on western North American plants*. Carnegie Institution of Washington Publication 520. Washington, DC: Carnegie Institution of Washington.

Foundational research in plant evolutionary ecology is contained in this publication (and several others) on experimental studies into the nature of intraspecific variation. Using experimental approaches they explore the genetic and environmental control of phenotypic traits in western North American species of *Potentilla*, *Achillea*, *Horkelia*, *Penstemon*, and *Artemisia*, among others.

- Dilek, Yildirim, Harald Furnes, and Karlis Muehlenbachs, eds. 2008. *Links between geological processes, microbial activities and evolution of life: Microbes and geology*. Dordrecht, The Netherlands: Springer.

The ten chapters explore the mode and nature of associations between geological processes and microbial activities, and their significance for the origin and evolution of life on Earth. Topics include microbial adaptation and evolution in extreme environments such as oceanic pillow lavas, hyaloclastites, deep subsurface, sub-seafloor, and Bahamian stromatolites.

- Harrison, Susan P., and Nishanta Rajakaruna, eds. 2011. *Serpentine: The evolution and ecology of a model system*. Berkeley: Univ. of California Press.

The nineteen chapters discuss how metal-enriched serpentinite habitats have been used or can be used to address major questions in Earth history, evolution, ecology, conservation, and restoration. Relevant evolutionary topics include intraspecific variation and local adaptation, speciation, phylogenetic analyses of endemism, and genomic approaches to the study of adaptation.

- Kruckeberg, Arthur R. 1986. An essay: The stimulus of unusual geologies for plant speciation. *Systematic Botany* 11:455–463.

Using western North America taxa as model systems, the paper describes possible modes of evolutionary diversification under the geodaphic influence. Although the focus is on plant-serpentinite relations, the modes and mechanisms of population differentiation and speciation outlined in the paper are generally applicable to species undergoing ecological divergence.

- Patzkowsky, Mark E., and Steven M. Holland. 2012. *Stratigraphic paleobiology: Understanding the distribution of fossil taxa in time and space*. Chicago: Univ. of Chicago Press.

The authors explore the exciting possibilities of stratigraphic paleobiology and demonstrate its great potential to examine critical questions about the history of life on Earth. The chapters provide an analytical framework for assessing the fossil record and paleontological literature by employing the principles of sediment accumulation.

- Rajakaruna, Nishanta. 2004. The edaphic factor in the origin of species. *International Geology Review* 46:471–478.

The relationship between adaptation to substrate and the origins of reproductive isolation is examined using ecologically divergent populations of western North American species of *Mimulus* and *Lasthenia*. The review makes a strong case for geodaphically driven speciation in flowering plants.

- Turesson, Göte. 1922. The species and the variety as ecological units. *Hereditas* 3.1: 100–113.

This foundational classic on the nature of intraspecific variation in plant species provides one of the earliest discussions of the ecotypic concept. The term ecotype, coined by the author, is used as an ecological subunit arising from genotypical response of a species to a particular habitat.

Physiology and Genetics

The study of the physiology and genetics of traits conferring adaptation to extreme geodaphic settings is a fast-developing area of research. Early-21st-century studies have shed light on novel physiological mechanisms for abiotic stress tolerance and their underlying genetic bases, providing tools for biotechnological applications in fields such as agriculture, forestry, and reclamation. In this regard, much attention has been directed at genetically modifying domesticated plants and animals (as well as microbes) to deal with abiotic stress, including stressors associated with climate change–related influences and geodaphic factors. [Jenks and Hasegawa 2014](#) is an excellent source for information on the physiology and genetics of plant adaptations to abiotic stressors such as salinity, flooding, temperature, and drought, while [Willmer, et al. 2004](#) is a useful resource for information on tolerance to heat, cold, salinity, and drought in animal species, including molecular insights into the mechanistic bases of adaptations to abiotic stressors animals encounter in various geodaphic settings. [Pointing and Belnap 2012](#) explores stress tolerance in microbes, particularly those exposed to cold and hot deserts: habitats that cover large portions of the world. The authors’ review discusses adaptations that confer tolerance to water stress in soil- and rock-colonizing species of cyanobacteria, chlorophytes, fungi, and heterotrophic bacteria. Tolerance to toxic heavy metals (often associated with anthropogenic contamination) has been a major area of research in the early 21st century. [Janssens, et al. 2009](#) reviews molecular mechanisms associated with heavy metal tolerance in invertebrate species, with a focus on physiological mechanisms of cadmium tolerance in

springtails. [DalCorso, et al. 2013](#) discusses the state-of-the-field for research in metal tolerance and accumulation, highlighting advances made due to methods such as transcriptomic-based DNA microarrays and proteomics. [Pérez-Clemente, et al. 2013](#) and [von Wettberg and Wright 2011](#) are excellent sources for advances in biotechnological methodology to investigate physiological and genetic bases for adaptations to edaphic stressors, including salinity and heavy metals. A chapter in [Rodriguez, et al. 2012](#) explores the role fungi play in conferring plant tolerance to abiotic stressors including drought, temperature, and salinity. This chapter, along with others included in the book, emphasizes the importance of paying attention to fungi in the study of plant geocology.

- dalCorso, Giovanni, Elisa Fasani, and Antonella Furini. 2013. [Recent advances in the analysis of metal hyperaccumulation and hypertolerance in plants using proteomics](#). *Frontiers in Plant Science* 4: Article ID 280.

This review is an excellent source of information regarding molecular pathways of heavy metal tolerance in metal hyperaccumulator and hypertolerant species. The focus is on advances in transcriptomic-based DNA microarrays and proteomics in the study of metal tolerance in plants.

- 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 insects and other invertebrates, highlighting research on metallothioneins and how their overexpression promotes cadmium tolerance in springtails (Collembola).

- Jenks, Matthew A., and Paul M. Hasegawa, eds. 2014. *Plant abiotic stress*. 2d ed. Ames, IA: Wiley.

The ten chapters in this comprehensive treatment on the physiology and genetics of plant adaptations to abiotic stresses (such as salinity, flooding, temperature, and drought) are written by experts in respective fields. Topics also include genomic approaches to the study of stress tolerance and epigenetic impacts on abiotic stress tolerance.

- Pérez-Clemente, Rosa M., Vicente Vives, Sara I. Zandalinas, María F. López-Climent, Valeria Muñoz, and Aurelio Gómez-Cadenas. 2013. Biotechnological approaches to study plant responses to stress. *BioMed Research International*. Article ID 654120.

The review summarizes progress on techniques in the study of plant responses to abiotic and biotic stress. Methods discussed include approaches in genomics, proteomics, metabolomics, and transgenic-based techniques. The importance of such biotechnological advances in stress tolerance to agricultural practices is also emphasized.

- Pointing, Stephen B., and Jayne Belnap. 2012. Microbial colonization and controls in dryland systems. *Nature Reviews Microbiology* 10:551–562.

The review illustrates the nature of microbial colonization in hot and cold deserts, and the adaptations that are important for the survival of soil- and rock-community associated microbes, including cyanobacteria, chlorophytes, fungi, and heterotrophic bacteria. Microbial influences in geochemical processes and microbial recovery and management are also a focus.

- Rodriguez, Russell J., Claire J. Woodward, and Regina S. Redman. 2012. Fungal influence on plant tolerance to stress. In *Biocomplexity of plant-fungal interactions*. Edited by Darlene Southworth, 155–163. Oxford: Wiley-Blackwell.

The role of fungi in plant tolerance to stresses such as drought, temperature, and salt is the focus of this chapter. Mechanisms of symbiotically conferred stress tolerance point to the fundamental role that soil microbes, such as fungi, play in tolerating edaphic and other abiotic stresses plants encounter in their habitats.

- von Wettberg, Eric, and Jessica W. Wright. 2011. Genomic approaches to understanding adaptation. In *Serpentine: The evolution and ecology of a model system*. Edited by Susan P. Harrison and Nishanta Rajakaruna, 139–154. Berkeley: Univ. of California Press.

The chapter describes advances in the fields of ionomics, metabolomics, proteomics, transcriptomics, and genomics that can be utilized to uncover the mechanistic and genetic basis for the tolerance of and adaptation to serpentinite- and other heavy metal-enriched soils.

- Willmer, Pat, Graham Stone, and Ian Johnston. 2004. *Environmental physiology of animals*. 2d ed. Oxford: Wiley-Blackwell.

The seventeen chapters explore all aspects of abiotic stress tolerance in animals, providing excellent summaries of tolerance to stresses associated with both terrestrial and aquatic environments. Discussions on tolerance to heat, cold, salinity, and drought are particularly relevant as well as molecular insights into the mechanistic bases of adaptations.

Reclamation and Restoration

Humanity's destruction of biological communities can be ameliorated by reclamation and restoration. Restoration ecology is a burgeoning and relatively new field: [van Andel and Aronson 2012](#) is a good introduction to the discipline and its goals, methods, and challenges. Geological considerations are important to reclamation and restoration efforts. For example, [Montgomery 2004](#) points out that, at the landscape level, geology and geomorphology are particularly important considerations in restoration of salmon runs. Particular geological substrates present special problems for restoration because they are inhabited by species or populations adapted to those substrates: the section on [Evolutionary Aspects](#) explores how geology can affect evolution on unusual substrates to produce locally adapted populations or species. As an example of these special restoration problems, [O'Dell and Claassen 2011](#) provides an overview of challenges and approaches useful for reclamation or restoration of serpentinite sites. As with restoration of most

sites on unusual geological materials, revegetation of serpentine sites should use plant materials obtained from populations that are adapted to those soils. In another example, [Gilardelli, et al. 2013](#) studies natural succession and restoration techniques on limestone quarries, illustrating the common positive correlation between economic expense and revegetation success. Fortunately, [Tropek, et al. 2010](#) points out that even spontaneous succession can be valuable for conservation objectives. There have been attempts to create sites functionally similar to those on special substrates on sites with normal soils. [Bonebrake, et al. 2011](#) attempted to modify nonserpentine soils to create soils similar to serpentine, and thus host their specialized flora (and discourage colonization by nonnative plants). They were only partly successful, demonstrating that such edaphic manipulation to date has limited application to restoration ecology. Geoengineering is a new field that proposes to manipulate Earth's ecological systems to reverse unintended changes caused by human activities. For example, [Caldeira, et al. 2013](#) summarizes proposals to address global climate change through geoengineering activities. The review [Power, et al. 2013](#) summarizes one potential geoengineering technique, showing how serpentinite may be used to sequester carbon dioxide. This technology takes advantage of the fact that carbonate minerals are produced during hydrothermal altering of serpentinite. Carbon could be sequestered by mining serpentinite for use in chemical reactors, or by injecting carbon dioxide solutions directly into serpentinite deposits. Large-scale implementation of these activities on serpentine landscapes, however, may create conservation challenges (see section on [Conservation](#)).

- Bonebrake, Timothy, Ryan Navratil, Carol Boggs, Scott Fendorff, Christopher Field, and Paul Ehrlich. 2011. Native and non-native community assembly through edaphic manipulation: Implications for habitat creation and restoration. *Restoration Ecology* 19:709–716.

The authors attempted to manipulate nonserpentine soils to create conditions that mimic serpentine soils, and thus could be useful for conservation of serpentine-associated plants and animals. They were only partially successful, pointing to the difficulty of artificially creating specialized edaphic conditions and the importance of preservation of natural systems.

- Caldeira, Jen, Govindasamy Bala, and Long Cao. 2013. The science of geoengineering. *Annual Review of Earth and Planetary Sciences* 41:231–256.

A review of proposals to address Earth's recent human-induced climate change through planetary-scale actions, including approaches to modify solar input as well as change atmospheric carbon dioxide concentrations.

- Gilardelli, Federica, Sergio Sgorbati, Sandra Citterio, and Rodolfo Gentili. 2013. Restoring limestone quarries: Hayseed, commercial seed mixture or spontaneous succession? *Land Degradation and Development*.

Illustrating the importance of how restoration “success” is defined, this study compares several methods of quarry restoration. Using a cost-benefit analysis, and defining success to include high biodiversity, the authors conclude that the most expensive method produces the best restoration success.

- Montgomery, David R. 2004. Geology, geomorphology, and the restoration ecology of salmon. *GSA Today* 14.11: 4–12.

This article describes how geology and geomorphology are vital components of the habitat of salmon and how these factors must be considered in efforts to restore salmon runs. It also provides a good entry into the literature regarding salmon ecology and restoration programs.

- O'Dell, Ryan E., and Victor Claassen. 2011. Restoration and revegetation of harsh soils. In *Serpentine: Evolution and ecology in a model system*. Edited by Susan P. Harrison and Nishanta Rajakaruna, 383–416. Berkeley: Univ. of California Press.

The chapter focuses on the restoration and revegetation of heavy metal–enriched serpentine sites. The authors summarize soil and vegetation manipulation methods used to restore degraded serpentine soil communities, and focus on critical steps needed for successful revegetation of degraded serpentine and other edaphically harsh settings.

- Power, Ian M., Siobhan A. Wilson, and Gregory M. Dipple. 2013. Serpentinite carbonation for CO₂ sequestration. *Elements* 9:115–121.

This review explains the process of carbonation using minerals found in serpentine areas. It explains how serpentine minerals could be used to sequester CO₂ at both local and global scales using either in situ or ex situ technologies.

- Tropek, Robert, Tomas Kadlec, Petra Karesova, et al. 2010. Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants. *Journal of Applied Ecology* 47:139–147.

This report shows that while technical restoration usually accelerates revegetation of mining sites, spontaneously recovering sites may provide better habitat for some species of conservation concern. Thus a mix of restoration techniques may be a preferred restoration strategy.

- van Andel, Jelte, and James Aronson, eds. 2012. *Restoration ecology: The new frontier*. 2d ed. Malden, MA: Blackwell Science.

This edited volume provides an overview of concepts and ecological underpinnings of restoration ecology, along with eight chapters that target restoration of particular types of freshwater and terrestrial communities.

Climate Change Consequences

Climate change is a major challenge to global biodiversity. [Cowie 2012](#) provides a comprehensive overview of the evidence regarding climate change, its causes and consequences for humans and other organisms, and potential actions to address it. Climate change impacts on biodiversity may be especially large for species with geographically restricted or patchy

distributions because, as climate changes, their habitat may disappear or be significantly altered. For example, low islands are very vulnerable to sea level rise. [Wetzel, et al. 2013](#) predicted major conservation impacts of sea level rise in Southeast Asia and Pacific regions. Effects of climate change are especially rapid in Arctic regions. Shrinkage of the extent of pack ice (an important habitat feature of mammals such as polar bears) is an example, and [Gormezano and Rockwell 2013](#) discusses changes in the diet of polar bears from the Hudson Bay area that are occurring as pack ice distribution changes. In mountainous regions, upward movement of climate zones may impact species. Exemplifying this threat is the American pika, found at high elevations in western North America. Upward shifts of mountain communities may cause the species' habitat to disappear in some locations: [Beever, et al. 2011](#) reports that the species is already experiencing local population extinctions and its range is shifting rapidly upward. Another challenge is if favorable climatic conditions move to areas to which a species cannot disperse, or to which a species cannot disperse rapidly enough. [Damschen, et al. 2012](#) uses species distribution models to examine extinction risk for plant species endemic to serpentine soil islands, but find surprisingly little extinction risk. However, the authors point out that many factors (including species' dispersal ability and the geographic distribution of soil islands) can affect this outcome. The section on [Biogeography](#) provides additional information regarding those factors. Climate change will likely affect biodiversity, but [Gilman, et al. 2011](#) points out that more diverse communities may be better able to withstand changes brought about by climate change. Finally, biologists often focus on the direct responses of organisms to climate change, but how humans respond to climate change may produce important indirect effects on biodiversity. Building on the example above of sea level rise effects on islands, [Wetzel, et al. 2012](#) shows that movements of human refugees in response to rising sea levels may have greater impacts on some species than the direct effects of sea level changes themselves.

- Beever, Erik, Chris Ray, Jenifer Wilkening, Peter Brussard, and Philip Mote. 2011. Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology* 17:2054–2070.

Using distribution records spanning a century, the authors document extinction and upward range expansion of the American pika in western North American mountains, illustrating the effects of climate change on montane species and communities.

- Cowie, Jonathan. 2012. *Climate change: Biological and human aspects*. 2d ed. Cambridge, UK: Cambridge Univ. Press.

This book provides an early-21st-century introduction to climate change past and present, including information on its impacts on humans and other organisms, its projected impacts, and efforts to address those impacts.

- Damschen, Ellen, Susan Harrison, David Ackerly, Barbara Fernandez-Going, and Brian Anacker. 2012. Endemic plant communities on special soils: Early victims or hardy survivors of climate change? *Journal of Ecology* 100:1122–1130.

The authors use species distribution models to predict the response of serpentine endemic species to climate change in California, United States, postulating high extinction risk.

They find relatively little extinction risk, and provide a literature review that can guide future explorations of climate change on special soils.

- Gilman, R. Tucker, Nicholas Fabina, Karen Abbott, and Nicole Rafferty. 2011. Evolution of plant-pollinator mutualisms in response to climate change. *Evolutionary Applications* 5.1: 2–16.

The authors use a modeling approach to study how changes in flowering time might impact plant-pollinator mutualisms. Among other conclusions, they find that more diverse pollinator communities buffer climate change effects, thus providing a benefit of maintaining pollinator biodiversity.

- Gormezano, Linda, and Robert Rockwell. 2013. What to eat now? Shifts in polar bear diet during ice-free season in western Hudson Bay. *Ecology and Evolution* 3:3509–3523.

The authors compare diets by comparing contents of scat collected in 2010 to scat collected forty years prior. They find diets have shifted as bears have adjusted to shrinkage of pack ice, but whether the species will be able to survive continued habitat changes is an actively debated issue.

- Wetzel, Florian, Helmut Beissmann, Dustin Penn, and Walter Jetz. 2013. Vulnerability of terrestrial island vertebrates to projected sea-level rise. *Global Change Biology* 19:2058–2070.

Using sea level rise projections and species distribution models, the authors estimate impacts of sea level rise on island species in Southeast Asia and Pacific areas. They find some island species are particularly susceptible to this threat and may become extinct as a result.

- Wetzel, Florian, W. Daniel Kissling, Helmut Beissmann, and Dustin Penn. 2012. Future climate change driven sea-level rise: Secondary consequences from human displacement for island biodiversity. *Global Change Biology* 18:2707–2719.

This study shows that sea level rise may have important effects on biodiversity because movements of humans in response to sea level changes will likely impact animal habitats, and thus create important secondary effects on biodiversity.

Conservation

Unusual geological substrates may harbor unique populations or species (see [Evolutionary Aspects](#)). Detecting unique biological elements is the first step toward their conservation: [Lin and Li 2014](#) describes five new species of armored spider from caves in Chinese karst habitat. [Wulff, et al. 2013](#) examines the flora of New Caledonia, finding that geological substrate is an important characteristic for species with few populations. The authors use species distribution models to predict locations of new populations and identify areas for conservation attention. Human uses of special substrates can put unique biological elements at risk: [Jacobi, et al. 2011](#)

illustrates this threat for plants in metal-mining areas of Brazil. While special geological substrates may be difficult for exotic species to colonize, exotics can create conservation problems in these areas. [Vallano, et al. 2012](#) demonstrates that human-caused nitrogen deposition may, by increasing fertility of serpentine soils and thus shifting competitive relationships to favor nonnatives, promote invasion by exotics. Besides invasion by nonadapted exotics, sites with special substrates may be vulnerable to invasion by exotics native to those substrates in other areas of the globe. This is a concern regarding the use of nonnative species in habitat restoration projects (see [Reclamation and Restoration](#)). An example is the case of smooth cordgrass, a native of eastern North American salt marshes used for salt marsh restoration in other areas (it also has spread accidentally). Effects in nonnative areas are mixed. For example, [Ma, et al. 2013](#) reports that in China, cordgrass promotes the spread of a threatened bird species that uses the grass as a nesting and feeding site. In contrast, [Nordby, et al. 2009](#) describes stands of introduced cordgrass as an ecological trap for a rare marsh sparrow subspecies (because it attracts birds to sites where nests are often destroyed by high tides). On a broader scale, geocology is an important consideration for management of protected areas. [Gordon, et al. 2002](#) points out how substrate affects ecology and management of alpine zones of several European mountain ranges, while [Montgomery 2004](#) (cited under [Reclamation and Restoration](#)) shows the importance of geological features in restoration of salmon runs. Another important conservation challenge is construction of networks of protected areas to preserve biodiversity. This issue is particularly important to conservation in geologically unusual areas, given the fragmented nature of many of these habitats (see [Biogeography](#)). [Clements, et al. 2006](#) describes the fascinating case of limestone karsts in Southeast Asia, showcasing their unique endemic fauna and flora as well as the conservation challenges facing their preservation.

- Clements, Reuben, Navjot Sodhi, Menno Schilthuizen, and Peter King. 2006. Limestone karsts of Southeast Asia: Imperiled arks of biodiversity. *BioScience* 56.9: 733–742.

The authors describe the geology, flora and fauna, human uses, and conservation challenges facing these often-spectacular formations. This article is an excellent example of the opportunities and difficulties for conservation of geologically unusual areas.

- Gordon, John E., Igor J. Dvorač, Christer Jonasson, Melanie Josefsson, Milena Kociánová, and Des B. A. Thompson. 2002. Geo-ecology and management of sensitive montane landscapes. *Geografiska Annaler: Series A, Physical Geography* 84:193–203.

Comparing three European alpine areas (in Scotland, Czech Republic, and Sweden), the authors demonstrate how consideration of geocological factors can inform management to protect biodiversity and address various human impacts such as deforestation, grazing, pasturing, recreation, pollution, and climate change.

- Jacobi, Claudia, Flávio do Carmo, and Iara de Campos. 2011. Soaring extinction threats to endemic plants in Brazilian metal-rich regions. *AMBIO* 40:540–543.

The authors point to the lack of protection of endemic plant species often found in areas targeted by mining operations in Brazil. They also point out the responsibility of

countries that have signed the Convention on Biological Diversity to inventory and protect their biodiversity.

- Lin, Yucheng, and Shuqiang Li. 2014. New cave-dwelling armored spiders (Araneae, Tetrablemmidae) from Southwest China. *ZooKeys* 388:35–76.

Describing five new species of armored spider in a new genus, the authors illustrate the potential for discovery of new species in geologically unusual areas, in this case caves in a limestone karst area of China.

- Ma, Zhijun, Xiaojing Gan, Chi-Yeung Choi, and Bo Li. 2013. Effects of invasive cordgrass on presence of Marsh Grassbird in an area where it is not native. *Conservation Biology* 28:150–158.

The authors show that smooth cordgrass provides suitable habitat for a rare bird species that is spreading into these marsh habitats, providing new areas for occupancy for the bird and thus providing at least some conservation benefit.

- Nordby, J. Cully, Andrew Cohen, and Steven Beissinger. 2009. Effects of a habitat-altering invader on nesting sparrows: An ecological trap? *Biological Invasions* 11:565–575.

A case study showing that a rare sparrow is attracted to dense stands of smooth cordgrass as nest sites, but these stands occur relatively low in the salt marsh topographic profile and thus are prone to being destroyed by flooding during high tide events.

- Vallano, Dena M., Paul C. Selmants, and Erika S. Zavaleta. 2012. Simulated nitrogen deposition enhances performance of an exotic grass relative to native serpentine grassland competitors. *Plant Ecology* 213:1015–1026.

Deposition of nitrogen may cause serpentine habitats to be more susceptible to invasion by nonnative, nonserpentine species. The authors show that nitrogen deposition may shift the competitive relationship between an invasive and native plant species so that the invasive is favored.

- Wulff, Adrien, Peter Hollingsworth, Antje Ahrends, et al. 2013. Conservation priorities in a biodiversity hotspot: Analysis of narrow endemic plant species in New Caledonia. *PLoS ONE* 8.9: e73371.

Finding that geological substrate is an important feature for species with narrow endemic status, the authors use species distribution models to map areas for conservation protection and to identify species under potential threat from mining operations.

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