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OXFORD BIBLIOGRAPHIES **IN ECOLOGY**
"SERPENTINE SOILS"
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Introduction

Serpentine soils are weathered products of a range of ultramafic rocks composed of ferromagnesian silicates. Serpentine more accurately refers to a group of minerals, including antigorite, chrysotile, and lizardite, in hydrothermally altered ultramafic rocks. Common ultramafic rock types include peridotites (dunite, wehrlite, harzburgite, lherzolite) and the secondary alteration products formed by their hydration within the Earth's crust, including serpentinite, the primary source of serpentine soil. Serpentine soils are generally deficient in plant essential nutrients such as nitrogen, phosphorus, potassium, and sulfur; have a calcium-to-magnesium (Ca:Mg) molar ratio of less than 1; and have elevated levels of heavy metals such as nickel, cobalt, and chromium. Although physical features of serpentine soils can vary considerably from site to site and within a site, serpentine soils are often found in open, steep landscapes with substrates that are generally shallow and rocky, often with a reduced capacity for moisture retention. Due to the intense selective pressure generated by such stressful edaphic conditions, serpentine soils promote speciation and the evolution of serpentine endemism, contributing to unique biotas worldwide, including floras with high rates of endemism and species with disjunct distributions. The biota of serpentine soils has contributed greatly to the development of ecological and evolutionary theory, as well as to the study of the genetics of adaptation and speciation. Plants growing on serpentine soils also provide genetic material for phytoremediation and phytomining operations. Habitats with serpentine soils are undergoing drastic changes due to ever-expanding development, deforestation, mining for heavy metals and asbestos, exotic-species invasions, climate change, and atmospheric deposition of previously limiting nutrients such as nitrogen. Such changes can have drastic impacts on serpentine floras and affect bacteria, fungi, and fauna associated with serpentine plants and soils. Habitats with serpentine soils provide ample opportunities for conservation- and restoration-oriented research directed at finding ways to better manage these biodiversity hotspots.

General Overviews

Serpentine-containing rocks, such as serpentinite, are an important cultural and historical material. Serpentinites can be easily worked and are used by many cultures for tool making, decorations, jewelry, ceremonial carvings, and amulets, as well as for magic, such as for protection from snake bites. Nickel, cobalt, chromium, and asbestos (e.g., chrysotile) are largely extracted from serpentine-containing rocks. Several significant treatments of serpentine soils, plants, and other biota, including serpentine as a model for ecological, evolutionary, and applied studies, have been published since 1975. Proctor and Woodell 1975 provides the first review of serpentine ecology, with a focus on factors that limit plant growth on serpentine soils. Brooks 1987 is a comprehensive treatment on serpentine floras from around the world, including individual chapters devoted to geology, soils, and nutritional and elemental stressors plants encounter when growing on serpentine soils. Roberts and Proctor 1992 complements Brooks 1987 in describing soil-plant relations of serpentine from sites in North America, Europe, Africa, Asia, and Australia. Jaffré 1980 provides a review of serpentine plants from endemic-rich New Caledonia, including tissue concentrations of heavy metals in plants found on serpentine soils. Brady, et al. 2005 is an extensive review of studies on the ecology and evolution of serpentine plants, with a particular focus on adaptation and speciation. Although restricted to western North America, Alexander, et al. 2007 is a thorough treatment of the geology, hydrology, and soils as well as the biodiversity (microbes, fungi, animals, and plants) of serpentine soils of California and western North America. The most recent treatment, Harrison and Rajakaruna 2011, is a collection of papers written by experts in their respective fields, asking what serpentine-associated studies have revealed about broader theoretical questions in geology, evolution, and ecology. The chapters on topics relating to earth history, evolution, ecology, and conservation confirm the value of serpentine as a model in multiple disciplines in the natural sciences.

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

Although geographically restricted, this book explores the ecology of serpentine habitats, focusing on soils and plants but including information on other organisms (animals, fungi, microorganisms) where feasible.

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.

An excellent review of plant adaptation to serpentine soils, this paper covers the defining features of serpentine soils and the mechanisms proposed for serpentine tolerance. It also addresses the evolution and genetics of serpentine adaptation and how speciation may occur in this type of habitat.

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

A classic overview of serpentine geology and ecology, this volume provides a summary of early work on this habitat type and includes information on soils, plants, animals, agriculture, and vegetation.

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 serpentine habitats have been used or can be used to address major questions in earth history, evolution, ecology, conservation, and restoration.

Jaffré, Tanguy. 1980. *Étude écologique du peuplement végétal des sol dérivés de roches ultrabasiques en Nouvelle Calédonie.* Travaux et Documents de L'ORSTOM 124. Paris: ORSTOM.

An early study of serpentine vegetation in a biological hotspot with very high endemism, this monograph contains information on the climate and soils, as well as the vegetation, of serpentine sites in New Caledonia. There is also extensive information about the elemental concentrations of plants growing on these soils, including hyperaccumulators.

Proctor, John, and Stanley R. J. Woodell. 1975. The ecology of serpentine soils. *Advances in Ecological Research* 9:255–366.

An early review of serpentine plant ecology that focuses on factors that may determine the relative infertility of serpentine soils, including Ca:Mg ratio, Mg/Ni interactions, metal toxicity, and low levels of major plant nutrients.

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.

An early summary of serpentine ecology in major global areas. After a brief geological review, thirteen contributed chapters cover serpentine 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 literature.

Journals

Papers regarding serpentine soils can be found in a variety of journals because this multidisciplinary and interdisciplinary topic is pertinent to the broad fields of geology,

mineralogy, petrology, and geochemistry and to all aspects of biology, ecology, evolution, conservation, and restoration. Important journals that publish papers involving serpentinite and associated rocks and serpentine soils include *International Geology Review* and *Soil Science Society of America Journal*. Recently, an entire issue of *Elements* was dedicated to exploring the origins, geodynamics, mineralogy, rheology, and tectonic significance of serpentinite rocks. In terms of biota associated with serpentine soils, including plants, fungi, bacteria, and invertebrate and vertebrate animals, pertinent papers can be found in journals with specialized taxonomic coverage, such as *American Journal of Botany* for plants, or in journals focusing on ecological phenomena, such as *Ecology*, or on evolutionary phenomena, such as *Evolution*. *Plant and Soil* publishes basic and applied studies relating to soil-plant/fungal relationships of serpentine plants, while *New Phytologist* periodically publishes papers on topics relating to physiological and evolutionary ecology of serpentine plants, including cross-kingdom interactions. The approaches to the study of serpentine soils and associated biota are diverse and are carried out worldwide, and, thus, papers associated with serpentine soils can be found in numerous international journals; we have listed a very small subset of important journals publishing original research and comprehensive reviews on serpentine-related topics.

American Journal of Botany.

Published by the Botanical Society of America, the journal covers all aspects of descriptive and experimental approaches to the study of plant biology, ecology, and evolution, including those relating to plants growing on serpentine soils.

Ecology.

Published by the Ecological Society of America, the journal publishes descriptive, comparative, and experimental approaches investigating topics relating to evolutionary ecology, population biology, physiological ecology, community ecology, and ecosystem studies, including those on serpentine soils.

Elements.

In this publication, subtitled *An International Magazine of Mineralogy, Geochemistry, and Petrology*, an entire issue (*Elements* 9.2, April 2013) was dedicated to describing the geochemistry and mineralogy of serpentinite rocks, including their significance in geodynamics, tectonics, origins of life, carbon sequestration, and metal extraction.

Evolution.

Published by the Society for the Study of Evolution, this journal publishes widely on evolutionary topics, including occasional papers on evolutionary aspects of serpentine plants.

International Geology Review.

The journal publishes research papers and reviews dealing with tectonics, economic geology, mineralogy, geochemistry, and petrology, including those of serpentinite and other ultramafic rocks.

New Phytologist.

Papers on various aspects of eco-physiology, evolutionary ecology, and cross-kingdom interactions of serpentine plants are periodically published in this journal, including papers focusing on metal-hyperaccumulating plants found on serpentine soils.

Plant and Soil.

This journal covers fundamental and applied aspects of plant-soil interactions, including those relating to serpentine soils.

Soil Science Society of America Journal.

The journal publishes research papers on descriptive, experimental, and applied aspects of the soil sciences, including papers on serpentine soils.

International Serpentine Ecology Conferences

These conferences provide an opportunity for the gathering of researchers from around the world, every two to four years, to share and discuss their most-recent findings relating to the broad and interdisciplinary field of serpentine ecology. Participants include botanists, zoologists, ecologists, pedologists, geologists, microbiologists, evolutionary geneticists, and conservation biologists. Serpentine ecology conferences have their origins in California; the first conference was held in 1991 at the University of California, Davis. Subsequently, conferences have been held in New Caledonia (1995), South Africa (1999), Cuba (2003), Italy (2006), Maine (2008), and Portugal (2012), always highlighting a region with intriguing serpentine soil-biota relations. The next conference is scheduled to take place in Malaysia (2014). The conferences have yielded six proceedings to date, highlighting the research that was presented in the first six conferences. Baker, et al. 1992 features the research presented in California; Jaffré, et al. 1997, in New Caledonia; Balkwill 2001, in South Africa; Boyd, et al. 2004, in Cuba; Chiarucci and Baker 2007, in Italy; and, most recently, Rajakaruna and Boyd 2009, in Maine.

Baker, Alan J. M., John Proctor, and Roger D. Reeves, eds. 1992. *The vegetation of ultramafic (serpentine) soils: Proceedings of the First International Conference on*

Serpentine Ecology, University of California, Davis, 19–22 June 1991. Andover, UK: Intercept.

In this first-ever proceedings of a serpentine conference, thirty-six papers describe serpentine soil-biota relations from all corners of the world, including North America, Central America, South America, Australia, New Zealand, Japan, South Africa, Italy, Ireland, the Philippines, the United Kingdom, and New Caledonia.

Balkwill, Kevin, ed. 2001. *Special issue: Third International Conference on Serpentine Ecology, Berg-en-Dal, Kruger National Park, South Africa, 22–28 March 1999. South African Journal of Science* 97.11–12.

Thirty-two papers dealing with serpentine soil-biota relations are found in these proceedings, with a focus on studies from southern Africa.

Boyd, Robert S., Alan J. M. Baker, and John Proctor, eds. 2004. *Ultramafic rocks: Their soils, vegetation, and fauna; Proceedings of the Fourth International Conference on Serpentine Ecology, 21–26 April 2003*. St. Albans, UK: Science Reviews, 2000.

Fifty descriptive and experimental studies on serpentine soils and biota from around the world are compiled in these proceedings, with a special focus on the geology and floristics of Cuban serpentines. All papers have both English and Spanish abstracts to aid their accessibility to Spanish-speaking scientists.

Chiarucci, Alessandro, and Alan J. M. Baker, eds. 2007. *Special issue: Advances in the ecology of serpentine soils. Plant and Soil* 293.1–2.

This special issue consists of seventeen original research papers (presented at the Fifth International Conference on Serpentine Ecology, held in Siena, Italy, in May 2006) on serpentine soil-plant-biota relations. The majority of papers in these proceedings deal with nickel-plant relationships.

Jaffré, Tanguy, Roger D. Reeves, and Thierry Becquer, eds. 1997. *The ecology of ultramafic and metalliferous areas: Proceedings of the Second International Conference on Serpentine Ecology, Nouméa, 31 July–5 August 1995*. ORSTOM Nouméa, Documents Scientifiques et Techniques III.2. Nouméa, New Caledonia: Centre ORSTOM de Nouméa.

A collection of forty-three papers are found in these proceedings, covering soils, flora and fauna, ecology and phytochemistry, plant physiology, and revegetation/restoration of serpentine sites. Papers are written in English or French, and thus the proceedings are at least partly accessible to readers of either language.

Rajakaruna, Nishanta, and Robert S. Boyd, eds. 2009. *Special issue: Soil and biota of serpentine: A world view; Proceedings of the Sixth International Conference on Serpentine Ecology. Northeastern Naturalist* 16.S5.

Thirty-two descriptive and experimental studies are compiled in this special issue, covering geology and pedology, floristics, microbiology, ecology, evolution, physiology, genomics, habitat restoration, and conservation.

Geology and Pedology

Rocks containing the serpentine group of minerals (hereafter, serpentine rocks or serpentinite) are present in almost all continents and island arcs and have their origin within the Earth's upper mantle. The olive-green color and smooth, scaly, or mottled appearance of many serpentine-containing rocks is the basis for the name serpentine: originating from the Latin *serpentinus* (meaning "serpent"). Serpentine rocks often form large massifs and belts or tabular bodies along continental margins, faults, and shear zones. Coleman and Jove 1992 provides a detailed account of the origin of serpentine, including how such rocks within the Earth's crust are directly linked to the tectonic emplacement of mantle rocks such as peridotite. It is also an important source for information on the mineralogy, petrology, weathering, and geographic distribution of serpentine rocks. Moores 2011 describes in historical detail how ophiolites (terrestrial assemblages that include ultramafic rocks such as serpentinite and peridotite) helped geologists understand seafloor spreading, a key piece of evidence in support of plate tectonic theory. A more recent account of the importance of serpentinite in continental rifting and oceanic spreading, including a role in nucleation and propagation of earthquakes, can be found in Hirth and Guillot 2013. Evans, et al. 2013 reviews our understanding of serpentinization (the process by which peridotite is hydrothermally altered to generate the serpentine group of minerals), describing what serpentinites are made of, why and how they form, and how their location of origin influences their geochemistry. McCollom and Seewald 2013 provides a fascinating account of how serpentinization creates strongly reducing conditions, including fluids that are enriched with hydrogen and methane; these are sources that chemosynthetic microorganisms can exploit for metabolic energy. An account of how serpentinites may aid our understanding of the origin and early evolution of life on Earth can be found in Cardace and Hoehler 2011 (see Bacteria, Fungi, and Lichens). Over 60 percent of the global nickel supply comes from nickel laterite ores produced from the intensive weathering of serpentinites found under humid, tropical conditions. Butt and Cluzel 2013 discusses the geological and environmental factors contributing to the formation of nickel laterites. Although focusing on California, the chapter "Serpentine Soil Distributions and Environmental Influences" in Alexander, et al. 2007 (cited under General Overviews) provides a useful summary of the taxonomy and developmental processes of serpentine soil. Another general treatment of serpentine pedology can be found in Brooks 1987 (see General Overviews). Alexander and DuShey 2011 discusses the importance of distinguishing between serpentine soils formed by the weathering of peridotite or serpentinite; these rocks are chemically similar yet mineralogically distinct, with appreciable differences in geomorphic and pedologic features.

Alexander, Earl B., and Jonna DuShey. 2011. Topographic and soil differences from peridotite to serpentinite. In *Special issue: Driving forces for global pedodiversity. Geomorphology* 135.3–4: 271–276.

This extensive survey of soils with peridotite and serpentinite parent materials revealed appreciable differences in geomorphic and pedologic features between these chemically similar but mineralogically distinct ultramafic rocks. The study suggests that it is important to distinguish between these two rocks when doing pedological and biological studies on serpentine habitats.

Butt, Charles R. M., and Dominique Cluzel. 2013. Nickel laterite ore deposits: Weathered serpentinites. *Elements* 9.2: 123–128.

A review of the factors influencing the formation and distribution of nickel laterites worldwide, including how the formation, mineralogy, and grade of the ore deposits are influenced by the interactive effects of lithology, tectonics, climate, and geomorphology.

Coleman, Robert G., and Carlos Jove. 1992. Geological origin of serpentinites. In *The vegetation of ultramafic (serpentine) soils: Proceedings of the First International Conference on Serpentine Ecology, University of California, Davis, 19–22 June 1991.* Edited by Alan J. M. Baker, John Proctor, and Roger D. Reeves, 469–494. Andover, UK: Intercept.

The chapter focuses on the mineralogy, petrology, weathering, and geographic distribution of serpentinites, including a discussion on plate tectonics and the origin of serpentinites.

Evans, Bernard W., Keiko Hattori, and Alain Baronnet. 2013. Serpentinite: What, why, where? *Elements* 9.2: 99–106.

A broad overview of the mineralogy of serpentinite, including kinetic aspects of serpentinization, the role of serpentinite in the recycling of elements, and locations of present-day serpentinization.

Hirth, Greg, and Stéphane Guillot. 2013. Rheology and tectonic significance of serpentinite. *Elements* 9.2: 107–113.

A detailed summary of the rheological properties of serpentinite and how these attributes are key to understanding earthquakes and other geophysical phenomena in subduction zones and oceanic 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 prime target for the study of the origin of life on Earth and life elsewhere in our solar system.

Moores, Eldridge M. 2011. Serpentinites and other ultramafic rocks: Why they are important for Earth's history and possibly for its future. In *Serpentine: The evolution and ecology of a model system*. Edited by Susan P. Harrison and Nishanta Rajakaruna, 3–28. Berkeley: Univ. of California Press.

The chapter describes the nature and geologic history of serpentine and its antecedent related rocks, including how regional differences in serpentinites relate to the history of a particular region. The author, a pioneer on ophiolite research, provides a personal account of how ophiolites influenced the theory of plate tectonics.

Bacteria, Fungi, and Lichens

Research on serpentine-associated microorganisms, including their diversity, ecology, and evolution, has given insight into factors and mechanisms responsible for generating below-ground microbial diversity, as well as into how serpentine settings may have been central to promoting the origin of life on Earth. Cardace and Hoehler 2011 evaluates how the serpentinization process itself can generate suitable habitat conditions for chemosynthetic microbes, including extremophile bacteria (also see McCollom and Seewald 2013, cited under Geology and Pedology). Takai, et al. 2005 uses molecular and physiological approaches to characterize a new species of bacterium isolated from a seafloor serpentine volcano. Work on extremophiles on serpentine settings has clear implications for ongoing research on extraterrestrial life on such planets as Mars, where ultramafic (peridotite) mantle rocks are also found. Oline 2006 uses a molecular approach to compare the diversity of bacteria species on serpentine and non-serpentine soils, showing that, at a lower taxonomic scale, soil bacteria of serpentine tend to be more similar to each other than they are to those of non-serpentine soils. Mengoni, et al. 2010 (cited under Ecological Aspects) is an excellent source for bacteria associated with metal-hyperaccumulating plants found on serpentine soils. Mycorrhizal fungi on serpentine have also received much attention (see Branco 2010 and Schechter and Bruns 2008, both cited under Habitat Reclamation and Restoration). Branco and Ree 2010 shows that, despite the extreme nature of the substrate, serpentine soils support a rich ectomycorrhizal fungal community, suggesting that fungi are uninhibited by the edaphic stressors characteristic of serpentine soils. Similarly, Daghino, et al. 2012 reports no clear correlation between fungal diversity and mineral composition of serpentine soils. In a rare study of macrofungi associated with serpentine soils, Maas and Stuntz 1969 documents distinct mycofloras for serpentine and non-serpentine soils, including a higher proportion of mycorrhizal species on serpentine compared to non-serpentine soils. Lichens have an intimate and often-inseparable relationship with their substrate; however, the serpentine-lichen relationship has received only limited attention. Favero-Longo, et al. 2004 presents the only available global review of serpentine-associated

lichens, while Rajakaruna, et al. 2012 compares lichen species on serpentine and non-serpentine rocks in the New Idria serpentinite mass in California, showing richer and more-distinct lichen assemblages on serpentine rocks.

Branco, Sara, and Richard H. Ree. 2010. Serpentine soils do not limit mycorrhizal fungal diversity. *PLoS ONE* 5.7: e11757.

Using nrDNA internal transcribed spacer (ITS) fragment and sequence analyses, the authors compare fungal communities between adjacent serpentine and non-serpentine soils. Serpentine soils supported rich fungal communities from all major fungal lineages, suggesting that serpentine soils do not constitute an extreme environment for ectomycorrhizal fungi.

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, Ca^{2+}-rich waters circulating in serpentine bodies) and how they provide novel ground for scientific investigation into extremophile evolution and life on other planets.

Daghino, Stefania, Claude Murat, Elisa Sizzano, Mariangela Girlanda, and Silvia Perotto. 2012. Fungal diversity is not determined by mineral and chemical differences in serpentine substrates. *PLoS ONE* 7.9: e44233.

Fungal isolation and direct DNA extraction revealed that some taxa were shared at four serpentine sites in the western Alps, while some taxa were specific to particular sites. However, the study shows a general lack of correlation between substrate mineral composition and the diversity of fungi at the four sites.

Favero-Longo, Sergio E., Deborah Isocrono, and Rosanna Piervittori. 2004. Lichens and ultramafic rocks: A review. *Lichenologist* 36.6: 391–404.

The first and only comprehensive review of lichens on serpentine worldwide, documenting that serpentine-associated lichens co-occur on Ca- and Si-rich rocks and are characterized by disjunct distributions. No consistent trends were detected in features typical of vascular plants on serpentine, such as paucity of species and occurrence of particular ecotypes.

Maas, John L., and Daniel E. Stuntz. 1969. Mycoecology on serpentine soil. *Mycologia* 61.6: 1106–1116.

The study shows distinct mycofloras for serpentine and non-serpentine soils in the Cascade Mountains of Washington State, where only 18 percent of 212 species collected were found on both soil types. A higher proportion of fungi were also mycorrhizal on serpentine compared to non-serpentine soils.

Oline, David K. 2006. Phylogenetic comparisons of bacterial communities from serpentine and nonserpentine soils. *Applied and Environmental Microbiology* 72.11: 6965–6971.

Comparing 16S rRNA clone libraries of samples from serpentine and non-serpentine soils at three sites in California and Oregon, soil bacterial communities from serpentine soils tended to be more similar to each other than they were to those of non-serpentine soils, and these differences were at a lower taxonomic scale.

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 serpentine and non-serpentine rocks in North America. Lichen assemblages of serpentine and non-serpentine rocks were significantly different at the species level but not at the generic level, with species richness significantly greater on the serpentine rocks.

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 subseafloor serpentine mud volcano, illustrating the potential of serpentine sites to harbor undescribed species.

Nonvascular and Vascular Plant Floristics

Although somewhat outdated, chapters in Baker, et al. 1992 (see International Serpentine Ecology Conferences) shed light on the floristics of serpentine of western North America, Newfoundland in Canada, Brazil, Cuba, New Caledonia, Queensland in Australia, New Zealand, Japan, South Africa, Italy, Shetland in the United Kingdom, and Ireland, adding to the descriptions of global serpentine floras documented in Brooks 1987 and Roberts and Proctor 1992 (both cited under General Overviews). While much attention has been paid to vascular plants of serpentine soils, only a handful of studies have examined the diversity of bryophytes on serpentine soils. Briscoe, et al. 2009 provides one such case, where distinct assemblages of bryophytes are reported from serpentine and adjacent granite. Serpentine species accumulated higher levels of heavy

metals and maintained lower Ca:Mg ratios, which is similar to vascular plants. Rajakaruna, et al. 2009, in the only review available for the geoecology of eastern North American serpentines, lists species of bryophytes and vascular plants known to occur on serpentine soils in the region. Western North America, on the other hand, has had a long tradition of botanical and ecological research on serpentine soils, thanks to over fifty years of exploratory and experimental studies by Professor Arthur Kruckeberg of the University of Washington (Seattle, Washington). Kruckeberg 1984 is a good source for early floristic studies that laid the foundation for the extensive serpentine-related research ongoing in California (see Harrison and Rajakaruna 2011, cited under General Overviews). Safford, et al. 2005 adds to the work started in Kruckeberg 1984, listing California's serpentine-associated taxa along with their degree of affinity to serpentine soils. Since Kruckeberg's pioneering studies, work by Susan Harrison (University of California, Davis) and colleagues since the early 1990s (also see relevant references cited under Ecological Aspects, Evolutionary Aspects, Climate Change Consequences, and Conservation) has contributed greatly to our understanding of the factors and mechanisms contributing to the diversity of serpentine habitats in California. Harrison and Inouye 2002 shows that California's serpentine-endemic flora has greater among-region diversity than within-region diversity, suggesting that a network of serpentine island preserves will be required to maintain the species diversity of California's serpentine soils.

Briscoe, Laura R. E., Tanner B. Harris, William Broussard, Eva Dannenberg, Fred C. Olday, and Nishanta Rajakaruna. 2009. Bryophytes of adjacent serpentine and granite outcrops on the Deer Isles, Maine, U.S.A. *Rhodora* 111.945: 1–20.

The authors report forty-three species of bryophytes on serpentine and twenty-six such species on granite. Fourteen species were shared in common. Tissue analyses suggest significantly higher Mg, Ni, and Cr and significantly lower Ca:Mg ratios for serpentine mosses compared to those from granite.

Harrison, Susan P., and Brian D. Inouye. 2002. High βdiversity in the flora of Californian serpentine "islands." *Biodiversity and Conservation* 11.10: 1869–1876.

The authors demonstrate that the flora endemic to serpentine soil in California shows unusually high "beta diversity" among regions, although "alpha" diversity within any given region is low. Their results confirm that conservation of an endemic-rich flora requires a network of sites to capture the spatial component of diversity.

Kruckeberg, Arthur R. 1984. *California serpentines: Flora, vegetation, geology, soils, and management problems*. University of California Publications in Botany 78. Berkeley: Univ. of California Press.

This is the first significant treatment of California's diverse serpentine flora, including information on soils and habitat management. It is a good source for floristic,

edaphic, and ecological information on the region's serpentine habitats, as well as for the several decades of floristic research undertaken by the author.

Rajakaruna, Nishanta, Tanner B. Harris, and Earl B. Alexander. 2009. Serpentine geoecology of eastern North America: A review. *Rhodora* 111.945: 21–108.

The review covers literature on serpentine soil and biota in eastern North America, from Newfoundland, Canada, to the southeastern United States, a region that has been largely ignored in global treatments of serpentine soil-biota relationships. Appendices list all known bryophytes, lichens, and vascular plant species known from the region's serpentine soils.

Safford, Hugh D., Joshua H. Viers, and Susan P. Harrison, 2005. Serpentine endemism in the California flora: A database of serpentine affinity. *Madroño* 52.4: 222–257.

The study generates a semiquantitative methodology for determining levels of serpentine affinity, including strictly endemic, broadly endemic, strong "indicator," etc., for California's rich serpentine flora. The database is useful for research in floristics, biosystematics, ecology, conservation, and land management.

Metal-Hyperaccumulator Plants

Metallophytes are plants that grow on soils that have naturally elevated levels of heavy metals, and, since high levels of some heavy metals often are associated with serpentine soils, many metallophytes are found on these soils. The term "hyperaccumulator" denotes metallophytes that take up and sequester relatively large amounts of metals in their aboveground tissues. Brooks 1998 provides an early overview of many aspects of hyperaccumulator plants, while van der Ent, et al. 2012 gives a summary of the definitions of hyperaccumulation of various heavy metals and points out that most hyperaccumulators accumulate nickel and occur on serpentine soils. Rascio and Navari-Izzo 2011 provides a broad summary of the physiology and ecology of metal-accumulating plants, including hyperaccumulators. Five hypotheses have been suggested to explain the evolution of metal hyperaccumulation by plants: the best-explored hypothesis is that of defense against herbivores and pathogens. Boyd 2007 reviews the evidence regarding the defense hypothesis and points to future research approaches and experimental needs. The very high metal concentrations of metal-hyperaccumulator plant tissues also create habitat for other organisms, such as herbivorous insects (see Boyd 2009, cited under Fauna) and bacteria (see Bacteria, Fungi, and Lichens). Hyperaccumulator plants may concentrate metal in the soil under their canopies to create high-metal habitats in which metal-resistant bacteria strains may be found, and, as shown in Mengoni, et al. 2010 (cited under Ecological Aspects), living tissues of hyperaccumulator plants may provide a niche for metal-tolerant bacteria. Hyperaccumulator plants are also receiving attention for their potential use in phytoextraction activities, such as phytoremediation and phytomining. Phytoremediation is the use of hyperaccumulator plants to remove metals from metal-contaminated soil,

while phytomining is the use of these plants to remove metals from naturally high-metal soils. In either case, the metals in the plant tissue can be considered "bio-ore" if the metals in them can be recovered. Chaney, et al. 2007 provides a review of potential phytoextraction technologies for several heavy metals, as well as discussion of the practical challenges of creating commercially viable technologies, while Boominathan, et al. 2004 reports a case study of how two nickel-hyperaccumulator species may be used to produce nickel bio-ore. Finally, Angle and Linacre 2005 gives an overview of potential negative environmental impacts associated with these new plant-based technologies.

Angle, J. Scott, and Nicholas A. Linacre. 2005. Metal phytoextraction—a survey of potential risks. *International Journal of Phytoremediation* 7.3: 241–254.

Summary of problems that may be created by phytoextraction technologies, including creating new weeds, toxicity of plants to native animals, and transfer of genetic material from phytoextraction crops to native plants.

Boominathan, Rengasamy, N. M. Saha-Chaudhury, Veena Sahajwalla, and Pauline M. Doran. 2004. Production of nickel bio-ore from hyperaccumulator plant biomass: Applications in phytomining. *Biotechnology and Bioengineering* 86.3: 243–250.

Using two nickel-hyperaccumulator species, the authors test the species' effectiveness in generating bio-ore when plant biomass is furnace treated. The bio-ore has high Ni concentrations but also relatively high Ca levels; the latter feature may be problematic for next steps in the metallurgical process.

Boyd, Robert S. 2007. The defense hypothesis of elemental hyperaccumulation: Status, challenges and new directions. *Plant and Soil* 293.1–2: 153–176.

This review evaluates evidence suggesting that hyperaccumulation evolved to defend plants against herbivores and pathogens.

Brooks, Robert R., ed. 1998. *Plants that hyperaccumulate heavy metals: Their role in phytoremediation, microbiology, archaeology, mineral exploration, and phytomining.* Wallingford, UK: CAB International.

The fifteen chapters in this edited volume provide a broad coverage of hyperaccumulator plants and the many fields of study in which they play a role.

Brooks, Robert R., Julian Lee, Roger D. Reeves, and Tanguy Jaffré. 1977. Detection of nickeliferous rocks by analysis of herbarium specimens of indicator plants. *Journal of Geochemical Exploration* 7:49–57.

This paper first used the term "hyperaccumulator" for plants that take up extraordinary quantities of metals into their tissues. It also illustrates the value of such plants for bioprospecting, the use of such plants as an indicator of the presence of metal ores, a topic that continues to generate interest today.

Chaney, Rufus L., J. Scott Angle, C. Leigh Broadhurst, Carinne A. Peters, Ryan V. Tappero, and Donald L. Sparks. 2007. Improved understanding of hyperaccumulation yields commercial phytoextraction and phytomining technologies. *Journal of Environmental Quality* 36.5: 1429–1443.

Overview of phytoextraction technologies for several heavy metals, with particular emphasis on nickel. The authors discuss important factors in the development of these technologies, including economic factors, development of effective phytoextractor species, factors affecting metal phytoavailability in soil, challenges recovering metal from plant biomass, and agronomic issues.

Rascio, Nicoletta, and Flavia Navari-Izzo. 2011. Heavy metal hyperaccumulating plants: How and why do they do it? And what makes them so interesting? *Plant Science* 180.2: 169–181.

The paper reviews the physiology, genetics, ecology, and applied aspects of metal-tolerant plants, especially those known to hyperaccumulate heavy metals. The figures illustrate transport systems constitutively overexpressed and/or with enhanced affinity to heavy metals and their role in uptake, root-to-shoot translocation, and vacuolar sequestration.

van der Ent, Antony, Alan J. M. Baker, Roger D. Reeves, A. Joseph Pollard, and Henk Schat. 2012. Hyperaccumulators of metal and metalloid trace elements: Facts and fiction. *Plant and Soil* 362.1–2: 319–334.

A timely review clarifying the circumstances in which the term "hyperaccumulator" is appropriate, outlining the conditions to be met when the term is used. It summarizes the main considerations for establishing metal hyperaccumulation in plants and redefines some of the terminology, including thresholds for the hyperaccumulation of various metals.

Fauna

The serpentine fauna has received much less scientific study than its flora. This was pointed out in Brooks 1987 (cited under General Overviews), an early compendium on serpentine habitats. Alexander, et al. 2007 (see General Overviews) contains a chapter devoted to serpentine animals, fungi, and bacteria, but it is clear that the literature on serpentine fauna is relatively depauperate. Chazeau 1997 examines patterns of serpentine endemism for New Caledonian animal groups, concluding that serpentine vegetation

provides an opportunity for adaptive radiation within animal groups because of low competition in these low-productivity habitats and (for herbivores) the availability of new habitats created by plant speciation. Overall, serpentine endemism among the animal orders ranged widely, from 0 to 61 percent; in contrast, about 50 percent of the flora of New Caledonia is endemic to serpentine. Certainly the greater mobility of animals suggests that they are less likely to develop specialized populations that are adapted to serpentine habitats. For example, Proctor and Whitten 1971 documents a large population of pocket gophers on serpentine soil but does not find that those animals differ from populations on non-serpentine sites. Wild 1975 explores the relationship between mound-building termites and serpentine soils in Africa, recording effects of the termites on the vegetation and also increased nickel and chromium concentrations in bodies of worker termites. There are serpentine-endemic animal species, most of which are specialist herbivores of serpentine-endemic plants. Boyd 2009 reviews the literature on these insects, some of which have high whole-body nickel concentrations and are termed "high-nickel" insects. The authors of Przybyłowicz, et al. 2003 used X-ray microanalysis to determine metal distributions within tissues, providing insight into physiological mechanisms of heavy-metal tolerance. Meindl, et al. 2013 uses the model plant *Mimulus guttatus* to show both direct and indirect effects of serpentine soil on pollination and florivory. Barro Cañamero, et al. 2004 contains a preliminary survey of the Lepidoptera from Cuban serpentine areas and identifies seventeen endemic species. Perhaps the best-studied serpentine-endemic animal is the Bay checkerspot butterfly. A series of classic studies by Paul Ehrlich and colleagues (reviewed in Ehrlich, et al. 1975) developed the concept of the metapopulation from studies of this serpentine-endemic insect, found on islands of serpentine outcrops scattered among inhospitable non-serpentine habitat types in the San Francisco Bay Area of California.

Barro Cañamero, Alejandro, Rayner Núñez Águila, and Krys Rodríguez-Fernández. 2004. The Lepidoptera of plant formations on Cuban ultramafics: A preliminary analysis. In *Ultramafic rocks: Their soils, vegetation and fauna; Proceedings of the Fourth International Conference on Serpentine Ecology, 21–26 April 2003*. Edited by Robert S. Boyd, Alan J. M. Baker and John Proctor, 223–226. St. Albans, UK: Science Reviews.

A survey of scientific collections, literature, and some field sites to document the Lepidoptera fauna of Cuban serpentine areas. The authors compile a list of 303 species and discover that at least 17 are endemic to serpentine sites.

Boyd, Robert S. 2009. High-nickel insects and nickel hyperaccumulator plants: A review. *Insect Science* 16.1: 19–31.

This review defines "high-nickel" insects, which have relatively high (> 500 micrograms/gram dry weight) nickel concentrations in their bodies. Almost all these insects feed directly on nickel-hyperaccumulator plants that are restricted to serpentine habitats.

Chazeau, Jean. 1997. Caractères de la faune de quelques milieux naturels sur sols ultramafiques en Nouvelle-Calédonie. In *Écologie des milieux sur roches ultramafiques et sur sols métallifères: Actes de la Deuxième Conférence Internationale sur l'Écologie des Milieux Serpentiniques, Nouméa, 31 juillet–5 août 1995*. Edited by Tanguy Jaffré, Roger D. Reeves and Thierry Becquer, 95–105. Documents Scientifiques et Techniques III.2. Nouméa, New Caledonia: Centre ORSTOM de Nouméa.

A landmark evaluation of patterns of serpentine endemism among animal orders (mostly invertebrates) in New Caledonia, this paper is a model for sorely needed faunistic evaluations of serpentine areas.

Ehrlich, Paul R., Raymond R. White, Michael C. Singer, Stephen W. McKechnie, and Lawrence E. Gilbert. 1975. Checkerspot butterflies: A historical perspective. *Science* 188.4185: 221–228.

A review of the early work of Ehrlich and colleagues on this serpentine-endemic butterfly species, covering fifteen years of investigations into its ecology.

Meindl, George A., Daniel J. Bain, and Tia-Lynn Ashman. 2013. Edaphic factors and plant–insect interactions: Direct and indirect effects of serpentine soil on florivores and pollinators. *Oecologia*.

Serpentine sites had lower amounts of flower damage but also lower levels of pollinator visitation. These differences were partly due to differences in the faunas of serpentine and non-serpentine sites and partly due to differences in plant size and chemical composition caused directly by soil differences.

Proctor, John, and Kenneth Whitten. 1971. A population of the valley pocket gopher (*Thomomys bottae*) on a serpentine soil. *American Midland Naturalist* 85.2: 517–521.

The authors document a high population density of gophers on serpentine soils and collect Ca/Mg ratio data from soil and corms of *Brodiaea*, a major gopher food plant. They conclude the gopher's diet has a relatively low Ca:Mg ratio.

Przybyłowicz, Wojciech J., Jolanta Mesjasz Przybyłowicz, Pawel Migula, Elżbieta Głowacka, Mirosław Nakonieczny, and Maria Augustyniak. 2003. Functional analysis of metals distribution in organs of the beetle *Chrysolina pardalina* exposed to excess of nickel by Micro-PIXE. In *Special issue: 8th International Conference of Nuclear Microprobe Technology and Applications. Nuclear Instruments and Methods in Physics Research B: Beam Interactions with Materials and Atoms* 210:343–348.

One of a series of papers that present the results of X-ray microanalysis to study the tissue-level localization of metals in animals, plants, and fungi from serpentine sites, this

study examines a high-nickel insect from South Africa. The authors conclude elimination of nickel by Malphigian tubules is an important adaptation for this beetle.

Wild, H. 1975. Termites and the serpentines of the Great Dyke of Rhodesia. *Transactions of the Rhodesia Scientific Association* 57.1: 1–11.

A detailed study of the association between termites (especially a mound-building species) and serpentine soils. Ant mounds had different (less extreme) soil chemistry than the surrounding soils and thus affected composition of the vegetation. Bodies of worker termites had high metal concentrations compared to soldier and queen termites.

Ecological Aspects

The often-sharp differences in habitat features between serpentine and adjacent non-serpentine areas have led to the suggestion that fragmented serpentine habitats form archipelagos in non-serpentine habitat seas. Harrison, et al. 2006 explores regional and local factors involved with plant richness on California serpentine sites, finding that outcrop area and isolation were less important than environmental factors such as rainfall and local vegetation features. Given the island nature of many serpentine habitats, it is appropriate that the metapopulation concept was developed by Paul Ehrlich and colleagues during studies of serpentine habitat fauna (see Ehrlich, et al. 1975, cited under Fauna). Kazakou, et al. 2008 hypothesizes that the high degree of endemism of serpentine floras is achieved via adaptations that allow species to tolerate serpentine site conditions and that these adaptations result in loss of competitive ability when serpentine populations are grown on non-serpentine soils. Moore and Elmendorf 2011 reviews the role of competition in serpentine endemism and concludes that more studies are needed of the complex factors that may be involved in determining the effects of competition in serpentine systems. As reviewed in Brady, et al. 2005 (see General Overviews), soil nutrient factors such as Ca and Mg levels (or their ratio) or levels of heavy metals (Ni or Cr) have received much attention as important stressors, but other features (drought) may also be important. Gustafson and Casper 2004 shows how changes in macronutrient availability can alter plant-microbe interactions and resulting community structure. Susceptibility to pathogens may reinforce endemism of serpentine species. Springer 2009 tests this "pathogen refuge" hypothesis for flax (*Hesperolinon*) species in California, finding that rust disease was less prevalent in species restricted to serpentine soils. Mengoni, et al. 2010 reviews the ecology of microbes associated with metal-accumulating plants, documenting how serpentine plants and their rhizospheric soils are specialized habitat for microbes. Studies of serpentine fauna are scarce, but heavy metals likely affect that component of serpentine communities. Visioli, et al. 2013 explores microarthropod diversity in Italian serpentine soils, finding that metal concentrations are negatively correlated with diversity. Another feature that may influence adaptation is substrate color. Porter 2013 reports a striking case of plant seed color matching substrate color on serpentine and non-serpentine soils. Presumably the color match was driven by seed predation, illustrating an understudied aspect of plant adaptation to serpentine habitats. Another contribution, in Strauss and Cacho 2013, shows a color match between

leaves and serpentine substrate, pointing to visual apparency as an important but underappreciated factor.

Gustafson, Daniel J., and Brenda B. Casper. 2004. Nutrient addition affects AM fungal performance and expression of plant/fungal feedback in three serpentine grasses. *Plant and Soil* 259.1–2: 9–17.

    The study finds that nutrient enrichment affects plant/soil microbial community feedback, leading to changes in plant and soil microbial community structure.

Harrison, Susan, Hugh D. Safford, James B. Grace, Joshua H. Viers, and Kendi F. Davies. 2006. Regional and local species richness in an insular environment: Serpentine plants in California. *Ecological Monographs* 76.1: 41–56.

    In a comprehensive investigation of the richness of serpentine plant species at multiple geographic scales, the authors compare the influences of spatial habitat structure and environmental features on local and regional species richness. They find local environment, regional richness, historical factors, and spatial structure to be important contributors to species richness.

Kazakou, Elena, Panayiotis G. Dimitrakopoulos, Alan J. M. Baker, Roger D. Reeves, and Andreas Y. Troumbis. 2008. Hypotheses, mechanisms and trade-offs of tolerance and adaptation to serpentine soils: From species to ecosystem level. *Biological Reviews* 83.4: 495–508.

    Early-21st-century work on serpentine ecology is highlighted, focusing on specific mechanisms of species tolerance and adaptation to serpentine soils, including their effects on species endemism, community structure, and ecosystem functioning.

Mengoni, Alessio, Henk Schat, and Jaco Vangronsveld. 2010. Plants as extreme environments? Ni-resistant bacteria and Ni-hyperaccumulators of serpentine flora. *Plant and Soil* 331.1–2: 5–16.

    The review examines how metal-accumulating plants from serpentine soils can serve as extreme habitats for metal-tolerant bacteria and how the study of this cross-kingdom interaction can provide new insights on microbial adaptation and evolution.

Moore, Kara A., and Sarah C. Elmendorf. 2011. Plant competition and facilitation in systems with strong environmental gradients. In *Serpentine: The evolution and ecology of a model system*. Edited by Susan P. Harrison and Nishanta Rajakaruna, 223–236. Berkeley: Univ. of California Press.

After considering experimental design of competition studies, the authors conclude that high levels of environmental heterogeneity on serpentine sites may affect the importance of competition along serpentine/non-serpentine gradients. They provide suggestions for future research approaches to studies of competition in serpentine systems.

Porter, Stephanie S. 2013. Adaptive divergence in seed color camouflage in contrasting soil environments. *New Phytologist* 197.4: 1311–1320.

This study shows remarkable matching of seed color to soil color in *Acmispon wrangelianus* both in serpentine and nearby non-serpentine habitats. The study suggests that selection for crypsis (to defend against seed predation) is the likely explanation, illustrating an understudied factor that may be involved in adaptation to serpentine habitats.

Springer, Yuri P. 2009. Do extreme environments provide a refuge from pathogens? A phylogenetic test using serpentine flax. *American Journal of Botany* 96.11: 2010–2021.

This test of a long-standing hypothesis about lesser levels of disease on serpentine soils reports evidence that serpentine habitats provide refuge from pathogen attack. The author finds this puzzling, with serpentine soils having low Ca:Mg ratios; yet, high levels of Ca often have been associated with increased pathogen resistance.

Strauss, Sharon Y., and N. Ivalú Cacho. 2013. Nowhere to run, nowhere to hide: The importance of enemies and apparency in adaptation to harsh soil environments. *American Naturalist* 182.1: E1–E14.

Focusing on the relatively open nature of some serpentine sites, the authors demonstrate greater attack rates both for plants and their herbivores from their respective enemies in these habitats. They conclude that visual apparency may lead to defense either by crypsis or increased levels of chemical defenses on these sites.

Visioli, Giovanna, Cristina Menta, Ciro Gardi, and Federica Delia Conti. 2013. Metal toxicity and biodiversity in serpentine soils: Application of bioassay tests and microarthropod index. *Chemosphere* 90.3: 1267–1273.

This study suggests that microarthropod diversity is less on serpentine soils with greater metal concentrations. Microarthropod diversity was also affected by concentration of soil organic matter, which covaried with metal concentration, suggesting that direct experiments will be needed to separate the effects of each facet.

Evolutionary Aspects

Due to the high degree of abiotic stress and insular nature of serpentine outcrops, serpentine-associated taxa are model organisms for the study of adaptation, ecotypic differentiation, and speciation. Von Wettberg and Wright 2011 (see Physiology and Genetics) shows how molecular methods have provided powerful tools to examine the genetic bases for adaptation to serpentine soils and to characterize the genes that may play a role in population differentiation and speciation. Turner, et al. 2010, by using the model genus *Arabidopsis*, shows polymorphisms for traits involved in Ca:Mg tolerance and heavy-metal detoxification in serpentine and non-serpentine populations. The authors' results suggest that parallel ecological adaptations can occur via the differentiation of the same polymorphism at serpentine-tolerant loci in geographically distinct serpentine-tolerant populations. O'Dell and Rajakaruna 2011 provides an extensive review of intraspecific variation known to occur in serpentine and non-serpentine populations of seventy-eight taxa from twelve plant families, documenting flowering-time differences to suggest potential for reduced gene flow between ecologically divergent populations. Kay, et al. 2011 evaluates evidence for the mechanisms of plant speciation and lists modes of reproductive isolation documented for seventeen pairs of serpentine and non-serpentine sister species or populations. The authors highlight the contributions that studies of serpentine plants, including *Mimulus, Layia, Collinsia, Helianthus, Noccaea*, and *Lasthenia*, have made to the general understanding of speciation, and they suggest directions for future research. Ecological specialization can greatly reduce gene flow between divergent populations, and Yost, et al. 2012 employs a reciprocal-transplant experiment to examine how local adaptation to edaphic regions within a serpentine outcrop can contribute to prezygotic isolation between closely related taxa. Moyle, et al. 2013 shows that postzygotic barriers (hybrid sterility) between adjacent serpentine and non-serpentine ecotypes can also contribute to reducing gene flow, illustrating another mechanism by which population differentiation can take place via edaphic specialization. By using molecular phylogenies, Anacker, et al. 2011 and Anacker 2011 take a meta-analysis approach to understanding patterns of diversification under the serpentine influence, including the roles that evolutionary and biogeographic histories and regional environmental conditions play in the evolution of serpentine endemism. Anacker and colleagues' analysis of phylogenies for twenty-three genera from California shows that serpentine endemics exhibit few transitions out of the endemic state, suggesting adaptation to serpentine and subsequent diversification can lead to an evolutionary "dead end." Research in Kolář, et al. 2012, however, suggests that serpentine lineages may not always represent evolutionary "dead ends" but, rather, are dynamic systems with a potential to further diversify via independent polyploidization and hybridization, even providing a pathway to radiate off serpentine soils.

Anacker, Brian L. 2011. Phylogenetic patterns of endemism and diversity. In *Serpentine: The evolution and ecology of a model system*. Edited by Susan P. Harrison and Nishanta Rajakaruna, 49–70. Berkeley: Univ. of California Press.

Global taxonomic and phylogenetic patterns of serpentine endemism are examined for endemic-rich regions (California, Cuba, and New Caledonia) versus endemic poor regions (Zimbabwe, Japan, and New Zealand) to explore how

evolutionary/biogeographic history and regional environmental conditions influence evolution of endemism.

Anacker, Brian L., Justen B. Whittall, Emma E. Goldberg, and Susan P. Harrison. 2011. Origins and consequences of serpentine endemism in the California flora. *Evolution* 65.2: 365–376.

Molecular phylogenies for twenty-three genera (784 taxa) and fifty-one serpentine endemics show a few transitions out of the endemic state. This is consistent with the widely hypothesized trade-off between serpentine tolerance and competitive ability, where serpentine endemics are physiologically capable of growing in non-serpentine soils but are less competitive.

Kay, Kathleen M., Kimiora L. Ward, Lorna R. Watt, and Douglas W. Schemske. 2011. Plant speciation. In *Serpentine: The evolution and ecology of a model system*. Edited by Susan P. Harrison and Nishanta Rajakaruna, 71–96. Berkeley: Univ. of California Press.

The chapter evaluates the theory and evidence for the mechanisms of plant speciation on serpentine soils. It highlights how studies of serpentine plants have contributed to the general understanding of speciation processes, and it suggests directions for future research.

Kolář, Filip, Tomáš Fér, Milan Štech, et al. 2012. Bringing together evolution on serpentine and polyploidy: Spatiotemporal history of the diploid-tetraploid complex of *Knautia arvensis* (Dipsacaceae). *PLoS ONE* 7.7: e39988.

To examine the link between polyploid evolution and serpentine differentiation, the authors investigate the evolutionary history of the polyploid complex of *K. arvensis*. Recurrent polyploidization appears to provide a pathway for tetraploid serpentine taxa to spread off serpentine habitats via hybridization with non-serpentine tetraploid lineages.

Moyle, Leonie C., Mia Levine, Maureen L. Stanton, and Jessica W. Wright. 2013. Hybrid sterility over tens of meters between ecotypes adapted to serpentine and non-serpentine soils. *Evolutionary Biology* 39.2: 207–218.

The study documents hybrid barriers developing in response to strong adaptive differentiation between adjacent and very recently diverged lineages of *Collinsia sparsiflora* (Scrophulariaceae) on and off serpentine soils, despite likely ongoing gene flow.

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

The chapter reviews how adaptation to chemically harsh soil conditions, including heavy-metal-enriched mine tailings and serpentine soils, can contribute to ecotypic differentiation and subsequent speciation. The discussion includes a useful summary of major trends in plant adaptation, as demonstrated by examples of intraspecific variation found among serpentine-tolerant species worldwide.

Turner, Thomas L., Elizabeth C. Bourne, Eric J. Von Wettberg, Tina T. Hu, and Sergey V. Nuzhdin. 2010. Population resequencing reveals local adaptation of *Arabidopsis lyrata* to serpentine soils. *Nature Genetics* 42.3: 260–263.

Serpentine and non-serpentine populations document soil-type-associated polymorphisms at heavy-metal detoxification and Ca and Mg transport loci, providing candidate genes for the study of serpentine adaptation. Results suggest ecological adaptation via parallel differentiation of the same polymorphism as well as convergent evolution via different polymorphisms at the same loci.

Yost, Jenn M., Teri Barry, Kathleen M. Kay, and Nishanta Rajakaruna. 2012. Edaphic adaptation maintains the coexistence of two cryptic species on serpentine soils. *American Journal of Botany* 99.5: 890–897.

The study demonstrates, via a reciprocal-transplant experiment, how small-scale and continuous edaphic gradients on a serpentine outcrop can contribute to local adaptation, leading to reproductive isolation and coexistence under parapatry of *Lasthenia californica* and *L. gracilis* (Asteraceae).

Physiology and Genetics

Serpentine soils are challenging habitats for plants, and there has been considerable interest in determining how they meet those challenges. The low Ca:Mg ratio of serpentine soils is a major challenge to plant growth, and mechanisms to tolerate that low ratio are important adaptations. These mechanisms include tolerance of high levels of soil Mg and reduced absorption of Mg or higher absorption of Ca. For example, Palm, et al. 2012 uses the model plant *Mimulus guttatus* to show that Mg exclusion does not explain the ability of serpentine plants to grow in hydroponic solutions with low Ca:Mg ratio. In addition, low macronutrient concentrations, high levels of some heavy metals, and low water availability have commonly been suggested as important factors. Overviews of serpentine plant ecology (see Ecological Aspects) provide summaries of the research behind each of these stress factors. While many studies focus on the effects of a single stress factor, these stress factors likely have combined effects. Murren, et al. 2006 shows both individual and combined effects of Ca:Mg ratio and water availability on traits of *Mimulus guttatus*. Tolerance of high levels of heavy metals has received a great amount of attention. Bothe 2012 summarizes the literature for plants, and Janssens, et al. 2009 provides a review of molecular mechanisms underlying metal tolerance in invertebrates. Gall and Rajakaruna 2013 reviews pertinent information on plants of the Brassicaceae, a family that includes many serpentine- tolerant and metal-hyperaccumulating plants.

There has also been considerable effort to understand the linkage between serpentine soil stress factors for plants and the genes that underlie plant adaptations to them. One approach used to identify genes involved in serpentine soil tolerance is to study quantitative trait loci (QTL). For example, Wu, et al. 2008 describes how the genus *Mimulus* has been developed as a model system to answer questions of ecological and evolutionary functional genomics, some of which have been addressed using QTL. Some of these efforts take advantage of populations of the widespread species *M. guttatus* that include some from serpentine sites (such as Palm, et al. 2012 and Murren, et al. 2006) or use endemic species of *Mimulus* found on serpentine sites. Another example of researchers using QTL is in Bratteler, et al. 2006, in which that approach is used to study the genetic basis of serpentine soil adaptation in *Silene vulgaris*. Von Wettberg and Wright 2011 suggests that advances in various fields of molecular biology may allow new approaches to studying serpentine plant physiology and the underlying genetics.

Bothe, Hermann. 2012. Plants in heavy metal soils. In *Detoxification of heavy metals*. Edited by Irena Sherameti and Ajit Varma, 35–57. Soil Biology 30. Berlin: Springer-Verlag.

Provides good general coverage of the mechanisms employed by plants to tolerate heavy metals, and so it makes an excellent gateway to the literature. The article also extends into applied uses of metal-tolerant plants in phytoremediation situations.

Bratteler, Martin, Christian Lexer, and Alex Widmer. 2006. Genetic architecture of traits associated with serpentine adaptation of *Silene vulgaris*. *Journal of Evolutionary Biology* 19.4: 1149–1156.

The authors use QTL mapping to identify genes involved in serpentine adaptation, finding fifteen QTLs with major effects.

Gall, Jillian E., and Nishanta Rajakaruna. 2013. The physiology, functional genomics, and applied ecology of heavy metal-tolerant Brassicaceae. In *Brassicaceae: Characterization, functional genomics and health benefits*. Edited by Minglin Lang, 121–148. Hauppauge, NY: Nova Science.

The review describes all aspects of heavy-metal tolerance in the Brassicaceae (mustard family), known to consist of many serpentine-tolerant species. Tables highlight ninety-three Brassicaceae species currently known to hyperaccumulate metals and metalloids, genes responsible for metal tolerance, and species genetically engineered for heavy-metal tolerance.

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.

Review focusing on insects and other invertebrates, highlighting early-21st-century work on metallothioneins and how their overexpression promotes cadmium tolerance in springtails (Collembola).

Murren, Courtney J., Larry Douglass, Amanda Gibson, and Michele R. Dudash. 2006. Individual and combined effects of Ca/Mg ratio and water on trait expression in *Mimulus guttatus*. *Ecology* 87.10: 2591–2602.

This study shows that important stress factors in serpentine sites may act either separately or together in affecting plant traits. The authors also find that some traits may evolve independently of these stress factors and that phenotypic plasticity is a major adaptive feature of this model plant species.

Palm, Emily, Kristy Brady, and Elizabeth Van Volkenburgh. 2012. Serpentine tolerance in *Mimulus guttatus* does not rely on exclusion of magnesium. *Functional Plant Biology* 39.8: 679–688.

In a reciprocal-transplant experiment of populations from serpentine and non-serpentine soils, the authors find non-serpentine plants unable to survive in serpentine soils. By using hydroponics to isolate Ca:Mg ratio, they find reduced growth of the non-serpentine plants at low Ca:Mg ratios but similar levels of Mg uptake.

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 recent 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 serpentine and other heavy-metal-enriched soils.

Wu, Carrie A., David B. Lowry, Arielle M. Cooley, Kevin M. Wright, Young W. Lee, and John H. Willis. 2008. *Mimulus* is an emerging model system for the integration of ecological and genomic studies. *Heredity* 100.2: 220–230.

In an overview of the research that is developing *Mimulus* as a model system for evolutionary genetics, the authors describe how habitat adaptations (including those to serpentine habitats), floral evolution, breeding system, and other traits can be studied by using genetic tools developed for *Mimulus*.

Environmental Health

Serpentine areas may negatively affect human health. First, elevated metal concentrations may occur in water from serpentine watersheds. Krám, et al. 2009 reports high Ni in streams draining from a serpentine watershed in central Europe. Even if serpentine soils are modified to allow crop growth, elevated soil metals may lead to high concentrations in the crops, creating human health concerns. Fernández, et al. 1999 reports elevated levels of Cr and Ni in crop plants grown on serpentine soils in Spain; these high levels were amended by adding organic matter to the soils. There is concern about metal transfer through food webs of serpentine communities, but there is little evidence this is a health threat. For example, Miranda, et al. 2009 examines tissue metal concentrations of cattle raised on a Spanish serpentine grassland, finding Ni and Cu levels that might affect animal health but are not high enough to threaten human health. Spread of metals into food webs may be greater in areas that host metal hyperaccumulators (see Metal-Hyperaccumulator Plants). The authors of Peterson, et al. 2003 conducted a pioneering study that showed elevated Ni levels in food webs involving a nickel-hyperaccumulator plant. Meindl and Ashman 2013 shows that high-metal nectar (such as made by a hyperaccumulator plant) can influence bee movements and affect plant reproduction. Some serpentine areas are associated with forms of asbestos (e.g., amphibole), which have been tied to lung cancers caused by airborne particle inhalation. Interestingly, organisms native to serpentine sites may remediate asbestos pollution problems. Daghino, et al. 2009 reports that certain rare fungi in Italian serpentine areas break down asbestos fibers. Revegetation of disturbed serpentine areas may also decrease asbestos fibers in the air: Favero-Longo, et al. 2009 demonstrates a 50 percent reduction in airborne fibers from areas that had 15–40 percent plant cover. Finally, serpentine areas may play a role in solving global climate change. A recent review in Power, et al. 2013 summarizes how the mineral serpentinite could be used to sequester carbon dioxide, an important greenhouse gas. This technology takes advantage of the fact that the serpentinization process (see Geology and Pedology) involves production of carbonate minerals during hydrothermal altering of serpentinite. Carbon sequestration could be done by mining the mineral and using it in chemical reactors, or by injecting solutions containing carbon dioxide into underground serpentine formations. While this may help address the planet's carbon dioxide pollution problem, the potential negative impacts of this technology on the biodiversity of serpentine areas are significant.

Daghino, Stefania, Francesco Turci, Maura Tomatis, Mariangela Girlanda, Bice Fubini, and Silvia Perotto. 2009. Weathering of chrysotile asbestos by the serpentine rock-inhabiting fungus *Verticillium leptobactrum*. *FEMS Microbiology Ecology* 69.1: 132–141.

The authors study a rare fungus that occurs on serpentine sites, conducting a phylogenetic analysis to confirm its classification and demonstrating its enhanced ability to degrade fibers of chrysotile asbestos (compared to another fungus isolated from agricultural soil). They suggest it may be useful in remediating asbestos pollution.

Favero-Longo, Sergio E., Enrica Matteucci, and Consolata Siniscalco. 2009. Plant colonization limits dispersion in the air of asbestos fibers in an abandoned asbestos mine.

In *Special issue: Soil and biota of serpentine: A world view; Proceedings of the Sixth International Conference on Serpentine Ecology. Northeastern Naturalist* 16.S5: 163–177.

Innovative study that demonstrates reduced asbestos fiber dispersion from plots that are partially covered by vegetation, indicating that revegetation can reduce health hazards from abandoned asbestos mine sites. The authors also compare revegetation effectiveness of several native species, finding an endemic *Thymus* species particularly effective for revegetation.

Fernández, S., Silvia Seoane, and A. Merino. 1999. Plant heavy metal concentrations and soil biological properties in agricultural serpentine soils. *Communications in Soil Science and Plant Analysis* 30.13–14: 1867–1884.

Investigating serpentine soils that have been heavily amended with organic matter to allow growth of crops, the authors explore relationships between soil and plant levels of heavy metals. They report elevated Cr and Ni in plant tissues and conclude that heavy metals in crops may be a human health hazard.

Krám, Pavel, Filip Oulehle, Veronika Štědrá, et al. 2009. Geoecology of a forest watershed underlain by serpentine in central Europe. In *Special issue: Soil and biota of serpentine: A world view; Proceedings of the Sixth International Conference on Serpentine Ecology. Northeastern Naturalist* 16.S5: 309–328.

In this examination of a serpentine forest site, the authors analyze rocks, soils, plants, and stream water and evaluate the stream community to produce a relatively comprehensive geoecological study. Tree growth was slow, and, despite relatively high Ni levels in stream water, the benthic macroinvertebrate community in the stream was relatively diverse.

Meindl, George A., and Tia-Lynn Ashman. 2013. The effects of aluminum and nickel in nectar on the foraging behavior of bumblebees. *Environmental Pollution* 177:78–81.

By using flowers with artificially contaminated nectar, the authors document no effect for aluminum but a significant effect for nickel. Bumblebee visits were shorter to flowers with nickel-amended nectar, and bees were more likely to seek flowers farther away. They also may ingest toxic levels of nickel.

Miranda, Marta, J. L. Benedito, I. Blanco-Penedo, C. López-Lamas, A. Merino, and M. López-Alonso. 2009. Metal accumulation in cattle raised in a serpentine-soil area: Relationship between metal concentrations in soil, forage and animal tissues. *Journal of Trace Elements in Medicine and Biology* 23.2: 231–238.

The paper evaluates chromium, copper, and nickel accumulation in cattle raised in a serpentine area in southwestern Europe. A relatively high percentage of cattle showed tissue levels of nickel and copper indicative of risk of toxicity. Accumulation of chromium in tissues was generally low and within the normal range.

Peterson, Lynsey R., Victoria Trivett, Alan J. M. Baker, Carlos Aguiar, and A. Joseph Pollard. 2003. Spread of metals through an invertebrate food chain as influenced by a plant that hyperaccumulates nickel. *Chemoecology* 13.2: 103–108.

One of the first demonstrations that heavy-metal plants can mobilize metals into food webs (in this case, nickel). This phenomenon has implications for phytoremediation/phytomining, which might mobilize metals and cause unanticipated environmental impacts.

Power, Ian M., Siobhan A. Wilson, and Gregory M. Dipple. 2013. Serpentinite carbonation for CO_2 sequestration. *Elements* 9.2: 115–121.

This review presents the chemistry of carbonation by using minerals from serpentine areas. It evaluates the leading proposed in situ and ex situ technologies that may be used to sequester CO_2 both at local and global scales.

Habitat Reclamation and Restoration

Serpentine sites are often less disturbed by humans than other areas due to their relatively low primary productivity. Serpentine areas can be greatly affected by mining or geothermal energy development, which may require establishing vegetation on currently unvegetated areas (reclamation). Nickel mining has been an important activity on serpentine sites in New Caledonia, and there is great interest in revegetating highly disturbed mine sites. Jaffré, et al. 1997 contains contributions (some in French) that discuss attempts to revegetate these sites. Less intense activities, such as recreation or grazing, may also result in a need for plant community restoration. Recovery of ecological functions of impacted areas can be an important goal of reclamation/restoration efforts and may also decrease hazards to human health. O'Dell and Claassen 2011 provides an overview of the challenges and approaches useful for reclamation or restoration of serpentine sites. Because of the unique edaphic features of serpentine soils, plant materials used on serpentine sites should be from populations adapted to those soils (serpentine ecotypes). For example, O'Dell and Claassen 2006 shows that *Achillea millefolium* forms ecotypes on serpentine soils and that the ecotype performs better when used for serpentine site restoration. Revegetation may depend on successful recovery of the mycorrhizal fungal community, and fungal communities of serpentine areas may differ significantly from non-serpentine sites. Schechter and Bruns 2008 shows that the same plant species growing on serpentine soils may have different mycorrhizal associates than when on non-serpentine soils. Contrastingly, Branco 2010 reports serpentine soils were not a strong barrier to colonization by ectomycorrhizal fungi, perhaps because their mutualism with plant roots buffers soil differences.

Serpentine sites often are more challenging to restore due to their relatively inhospitable nature, which can slow the timeframe for recovery. Ironically, management steps such as fertilization to speed vegetation recovery can have unintended negative impacts by encouraging non-native species and favoring them in the competitive balance. Slingsby, et al. 2001 shows just such a fertilization effect from a cold-climate Scottish site but notes that the changes were temporary when examined from the perspective of a fifteen-year data set. Rajkumar, et al. 2009 suggests paying more attention to bacteria in the restoration of metal-enriched sites. Other ecological factors (e.g., fire frequency) may also be important. In serpentine barrens in the eastern United States, as described in Arabas 2000, lack of fire has resulted in woody invasion. In other cases, such as in New Caledonia, too-frequent fire in humid serpentine forests can convert serpentine forest into degraded scrub.

Arabas, Karen B. 2000. Spatial and temporal relationships among fire frequency, vegetation, and soil depth in an eastern North American serpentine barren. *Journal of the Torrey Botanical Society* 127.1: 51–65.

In an investigation of vegetation changes spanning more than fifty years, the author documents forest encroachment on serpentine savanna areas. Prescribed fire may be able to reverse the observed succession trends.

Branco, Sara. 2010. Serpentine soils promote ectomycorrhizal fungal diversity. *Molecular Ecology* 19.24: 5566–5576.

By using an innovative reciprocal-transplant experiment, the author finds a surprising lack of specialization of ectomycorrhizal fungi communities colonizing oak seedling roots. She concludes that serpentine soils are not a strong barrier to colonization, and she finds no evidence of serpentine specialist fungal species.

Jaffré, Tanguy, Roger D. Reeves, and Thierry Becquer. 1997. *Écologie des milieux sur roches ultramafiques et sur sols métallifères: Actes de la Deuxième Conférence Internationale sur l'Écologie des Milieux Serpentiniques, Nouméa, 31 juillet–5 août 1995*. Documents Scientifiques et Techniques III.2. Nouméa, New Caledonia: Centre ORSTOM de Nouméa.

This collection of forty-three papers covers a wide variety of serpentine topics, including a section of nine papers on revegetation of serpentine soils. Four papers target revegetation of the nickel mines of New Caledonia and provide overviews of the extensive work done there for this purpose.

O'Dell, Ryan E., and Victor Claassen. 2006. Serpentine and nonserpentine *Achillea millefolium* accessions differ in serpentine substrate tolerance and response to organic and inorganic amendments. *Plant and Soil* 279.1–2: 253–269.

Demonstrating the superior performance for revegetation of plants from a serpentine site, the authors also show the importance of soil amendments to boost revegetation success. They show that the serpentine plants have better Ca translocation abilities and therefore are better able to tolerate the low Ca:Mg ratio of serpentine sites.

O'Dell, Ryan E., and Victor Claassen. 2011. Restoration and revegetation of harsh soils. In *Serpentine: The evolution and ecology of 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 ecosystems. The discussion highlights soil and vegetation manipulation methods used to restore partially degraded serpentine soils, focusing on steps that are critical to successful revegetation of severely degraded serpentine and other edaphically harsh settings.

Rajkumar, Mani, Majeti N. V. Prasad, Helena Freitas, and Noriharu Ae. 2009. Biotechnological applications of serpentine soil bacteria for phytoremediation of trace metals. *Critical Reviews in Biotechnology* 29.2: 120–130.

The review points to the need for additional studies of microbes on serpentine soils in order to find metal-tolerant microorganisms that can aid in the phytoremediation of metal-contaminated sites.

Schechter, Shannon P., and Thomas D. Bruns. 2008. Serpentine and non-serpentine ecotypes of *Collinsia sparsiflora* associate with distinct arbuscular mycorrhizal fungal assemblages. *Molecular Ecology* 17.13: 3198–3210.

The authors demonstrate how different the fungal assemblages are between serpentine and non-serpentine populations of this herb species, implying that soil type has a strong influence on mycorrhizal assemblages.

Slingsby, David R., John Proctor, and Stephen P. Carter. 2001. Stability and change in ultramafic fellfield vegetation at the Keen of Hamar, Shetland, Scotland. *Plant Ecology* 152.2: 157–165.

A long-term (fifteen-year) study that shows surprisingly little successional change on this site, even after a fertilization experiment modified macronutrient supplies. Eutrophication due to raising of cattle on the site increased cover by grasses, but that change also was short lived once that disturbance ceased.

van der Ent, Antony, Alan J. M. Baker, Max M. J. van Balgooy, and Aiyen Tjoa. 2013. Ultramafic nickel laterites in Indonesia (Sulawesi, Halmahera): Mining, nickel

hyperaccumulators and opportunities for phytomining. *Journal of Geochemical Exploration* 128:72–79.

Indonesia has some of the largest surface exposures of serpentine bedrock in the world, and the paper describes the potential for the use of native species for mine restoration, including the extraction of residual nickel via phytomining.

Climate Change Consequences

Edaphically specialized plants may face a high risk from climate change due to the narrow limits of their habitat niches and their lower competitive ability compared to soil generalist species. Harrison, et al. 2009 calls for a greater need for incorporating serpentine and other edaphic floras in ecological research, climate change modeling, and conservation planning, because these plant communities are important contributors both to regional and global biodiversity. By using molecular phylogenies and environmental data, Anacker and Harrison 2012 shows that serpentine endemism in California is often associated with transitions to regions with favorable climates and greater habitat availability, illustrating how climate and disturbance regimes can influence the origin of serpentine endemics. Damschen, et al. 2011 explores how ecological attributes such as small and patchy distributions, increased stress tolerance, and reduced competitiveness against soil generalists, all characteristic of serpentine and other edaphic floras, can influence how edaphic specialists will respond to climate change scenarios. Further, Damschen, et al. 2012 argues how ecological research, including analyses of functional traits and ecological and evolutionary plasticity, across spatial and temporal scales, is critical to assess the efficacy of conservation planning for better managing edaphically specialized floras under climate change. Hobbs, et al. 2007 echoes these sentiments, pointing to the need for long-term studies to evaluate plant community–level responses to climate and disturbance. In addition to predicted changes in precipitation and temperature, climate change is also contributing to increased atmospheric deposition of previously limiting plant nutrients, particularly nitrogen. Weiss 1999 was the first study to highlight how nitrogen deposition can lead to invasive species encroachment in nutrient-poor serpentine grasslands in California. Since this pioneering paper, much research has been conducted on how nutrient deposition and disturbance contribute to species-level and community-level dynamics on serpentine outcrops in California. Esch, et al. 2013 examines how grazing and nitrogen deposition contribute to exotic species cover (also see Vallano, et al. 2012, cited under Conservation), microbial diversity, and nutrient cycling on serpentine soils, showing the possibility for large-scale shifts in species composition and population-level dynamics in serpentine habitats under predicted climate change scenarios.

Anacker, Brian L., and Susan P. Harrison. 2012. Climate and the evolution of serpentine endemism in California. *Evolutionary Ecology* 26.4: 1011–1023.

The study examines whether evolutionary transitions to serpentine endemism are associated with transitions to more-favorable environments. Transitions to endemism

were strongly associated with transitions to regions with more-benign climates, when originating from serpentine-intolerant ancestors, and to regions with greater habitat availability, when originating from serpentine-tolerant and -intolerant ancestors.

Damschen, Ellen I., Susan P. Harrison, David D. Ackerly, Barbara M. Fernandez-Going, and Brian L. Anacker. 2012. Endemic plant communities on special soils: Early victims or hardy survivors of climate change? *Journal of Ecology* 100.5: 1122–1130.

    The authors show that to better assess climate change risk to specialized edaphic floras, ongoing research efforts should incorporate functional trait analyses, evaluate the role of evolutionary and ecological plasticity, examine responses across spatial and temporal scales, and assess the efficacy of managed relocation efforts.

Damschen, Ellen I., Susan P. Harrison, Barbara M. Going, and Brian L. Anacker. 2011. Climate change and plant communities on unusual soils. In *Serpentine: The evolution and ecology of a model system*. Edited by Susan P. Harrison and Nishanta Rajakaruna, 359–383. Berkeley: Univ. of California Press.

    The chapter discusses ecological attributes shared by serpentine and other edaphically specialized plants and communities, shedding light on why edaphically restricted floras may respond differently to climate change scenarios than those on "normal" soils.

Esch, Ellen H., Daniel L. Hernández, Jae R. Pasari, Rose S. G. Kantor, and Paul C. Selmants. 2013. Response of soil microbial activity to grazing, nitrogen deposition, and exotic cover in a serpentine grassland. *Plant and Soil* 366.1–2: 671–682.

    The study shows that grazing intensity and soil N availability affects the soil microbial community indirectly via effects on exotic-species cover and associated changes in nutrient cycling. Additionally, grazing directly affects soil community function.

Harrison, Susan P., Ellen I. Damschen, and Barbara M. Going. 2009. Climate gradients, climate change, and special edaphic floras. In *Special issue: Soil and biota of serpentine: A world view; Proceedings of the Sixth International Conference on Serpentine Ecology. Northeastern Naturalist* 16.S5: 121–130.

    The authors propose a conceptual framework for how serpentine-endemic species will encounter climate change, including three potential tests of its predictions. This pioneering paper calls for greater attention to edaphically specialized floras when considering conservation options under future climate change scenarios.

Hobbs, Richard J., Susan Yates, and Harold A. Mooney. 2007. Long-term data reveal complex dynamics in grassland in relation to climate and disturbance. *Ecological Monographs* 77.4: 545–568.

The results of this long-term study on the dynamics of a serpentine annual grassland in Northern California emphasize the importance of longer-duration observations in providing a context for shorter-term experiments and in allowing analysis of plant community responses to climate variation and disturbance, particularly in the face of ongoing global change.

Weiss, Stuart B. 1999. Cars, cows, and checkerspot butterflies: Nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conservation Biology* 13.6: 1476–1486.

One of the earliest papers documenting that serpentine grasslands near San Francisco, California, have been invaded by the exotic grasses as the result of nitrogen deposition, primarily via fossil fuel emissions in central and coastal California.

Conservation

Serpentine areas have high priority for biodiversity conservation because of the relatively large numbers of endemic species and ecotypes. Conservation of the biota of serpentine areas faces many challenges. Whiting, et al. 2004 and Baker, et al. 2010 list some of those conservation threats and also point out the importance of conserving the biodiversity of serpentine plant species, in part because of the value of their genetic resources for potential uses such as phytoremediation and phytomining. Compared to other habitat types, serpentine areas may be relatively resistant to invasion by non-natives because of their relatively inhospitable habitat features. In the relatively well-studied Californian serpentines, Harrison, et al. 2006 shows that non-native plant species had a relatively small influence on the richness of serpentine-endemic species. This inherent resistance may be affected by some human activities. Vallano, et al. 2012 demonstrates that nitrogen deposition increases soil fertility, shifting the competitive relationships to favor non-natives and promoting invasion by exotics. The naturally occurring, highly fragmented spatial relationships among sites across a landscape can also influence conservation efforts. Saccani, et al. 2007 is a booklet containing a brief description of serpentine reserves within northern Italy. Thorne, et al. 2011 uses a California serpentine area as an example of systematic conservation planning. In the United States, some rare serpentine soil species are protected by the Endangered Species Act, and this protection triggers development of a recovery plan. As an example, Elam, et al. 1998 is the recovery plan for twenty-eight species of animals and plants that occur mainly on scattered serpentine areas around the San Francisco Bay of California. Such recovery plans contain much useful information, including a literature review, a status report on each species (including conservation threats), recovery objectives for each species, and a strategy for species conservation. Finally, some studies of serpentine plants have addressed the ecological effects of the fragmented nature of serpentine areas on plant population

biology, because they may have conservation management implications. Wolf 2001 studies the reproductive ecology of two serpentine-endemic species on large and small serpentine outcrops, determining that one was restricted to seeps microhabitats. Wolf concluded that conservation management of these two species would require different but complementary approaches.

Baker, Alan J. M., Wilfried H. O. Ernst, Antony van der Ent, Françoise Malaisse, and Rosanna Ginocchio. 2010. Metallophytes: The unique biological resource, its ecology and conservational status in Europe, central Africa and Latin America. In *Ecology of industrial pollution*. Edited by Lesley C. Batty and Kevin B. Hallberg, 7–40. Ecological Reviews. Cambridge, UK: Cambridge Univ. Press.

A broad overview of heavy-metal-tolerant plants from particular geographic regions, this chapter brings attention to the need to conserve these plants for their scientific value as well as their value in developing applied technologies.

Elam, Diane R., David H. Wright, and Bradley Goettle. 1998. *Recovery plan for serpentine soil species of the San Francisco Bay Area*. Portland, OR: US Fish and Wildlife Service, Region 1.

Excellent example of a recovery plan prepared for rare serpentine species occurring near a major human population center. Fourteen federally listed species and another fourteen species of conservation concern are included in this more than 330-page-long document, which is a rich summary of available biological information on each species.

Harrison, Susan, James B. Grace, Kendi F. Davies, Hugh D. Safford, and Joshua H. Viers. 2006. Invasion in a diversity hotspot: Exotic cover and native richness in the Californian serpentine flora. *Ecology* 87.3: 695–703.

In an analysis of an extensive data set, the authors find no evidence that exotic plant species cover reduces richness of native herb species. They conclude that exotic species have mainly localized impacts, and as of yet there is no detectable decline in the richness of the unique California serpentine flora.

Saccani, Andrea, Alessandro Chiarucci, and Mauro Mariotti, eds. 2007. *Un viaggio nell'Italia delle "pietre verdi": Aree protette—flora e vegetazione*. Parma, Italy: Coordinamento Aree Protette Ofiolitiche Technografica.

Privately published in Italian and English, this booklet describes a network of protected serpentine areas in the Northern Apennine Mountains of Italy. The geographic setting, climate, vegetation, and other features of each reserve are described, along with discussion of how the network is coordinated to preserve biodiversity of the area.

Thorne, James H., Patrick R. Huber, and Susan Harrison. 2011. Systematic conservation planning: Protecting rarity, representation, and connectivity in regional landscapes. In *Serpentine: The evolution and ecology of a model system*. Edited by Susan Harrison and Nishanta Rajakaruna, 309–328. Berkeley: Univ. of California Press.

By using data on existing conservation areas, serpentine occurrences, and plant distributions, the authors demonstrate how two preserve design algorithms (Marxan and least-cost corridor analysis) can be applied to achieve conservation goals in an example serpentine area in Northern California.

Vallano, Dena M., Paul C. Selmants, and Erika S. Zavaleta. 2012. Simulated nitrogen deposition enhances the performance of an exotic grass relative to native serpentine grassland competitors. *Plant Ecology* 213.6: 1015–1026.

Human-caused nitrogen deposition may change serpentine habitats so that they are more susceptible to invasion by non-native, non-serpentine species. This growth chamber study shows nitrogen deposition may act indirectly by shifting the competitive balance between an invasive and several native plant species.

Whiting, Stephen N., Roger D. Reeves, David Richards, et al. 2004. Research priorities for conservation of metallophyte biodiversity and their potential for restoration and site remediation. *Restoration Ecology* 12.1: 106–116.

This paper stresses the need to protect heavy-metal-tolerant plants because they and their genes provide the basis for reclamation/restoration of heavy-metal-contaminated sites. The authors discuss six important questions about knowledge gaps, threats to metallophytes, their uses, and ethical issues raised by those uses.

Wolf, Amy. 2001. Conservation of endemic plants in serpentine landscapes. *Biological Conservation* 100.1: 35–44.

In a study of two California serpentine-endemic species, Wolf shows that detailed study of reproductive ecology is needed to design conservation strategies for plants in serpentine landscapes. Her work illustrates the need to conserve multiple populations and a broad range of microhabitats.