Advances in Serpentine Geoecology: A Retrospective

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Serpentine habitats have long provided model settings for geoecological research (reviewed in Alexander et al. 2007, Brady et al. 2005, Brooks 1987, Kazakou et al. 2008, Kruckeberg 1984, Proctor and Woodell 1975, Rajakaruna et al 2009). Serpentine loosely refers to a broad group of minerals associated with the weathering of ultramafic (high iron and magnesium-rich) rocks found along continental margins and orogenic belts. Soils associated with such rocks often differ from more widespread soils, being less fertile and having high concentrations of some heavy metals. The unique geochemistry of serpentine soils generates habitats worldwide that are biologically unique, providing model settings for research on how geology and soils can shape the biotic world around us.

Serpentine outcrops worldwide are known to harbor high rates of plant endemism (Brooks 1987, Kruckeberg 2002). For example, of the 1410 plant species endemic to California, 176 (12.5%) are restricted to serpentine (Safford et al. 2005), a substrate covering less than 1.5% of the state. This number is remarkably high given only 669 taxa are associated with serpentine soils in California. Thus, it is no surprise that serpentine floras are well-studied in California and other parts of western North America (Alexander et al. 2007, Harrison and Viers 2007), not only for their taxonomic value but also for their usefulness in testing ecological and evolutionary scenarios. Additional examples include the tropical islands of New Caledonia and Cuba, which also provide remarkable cases of serpentine endemism (Boyd et al. 2004, Brooks 1987, Kruckeberg 2002). In New Caledonia, 3178 taxa, approximately half the native flora, are endemic to serpentine soils (Jaffré 1992). In Cuba, 920 species, approximately one-third of the taxa endemic to Cuba, are found solely on serpentine soils (Borhidi 1992). Similar restrictions and notable floristic associations are also found in serpentine areas of the Mediterranean, Africa, Australasia, and Asia (Baker et al. 1992, Balkwill 2001, Boyd et al. 2004, Brooks 1987, Chiarucci and Baker 2007, Jaffré et al. 1997).

Thus, it was no surprise that the recently concluded Sixth International Conference on Serpentine Ecology (www.coa.edu/serpentine) at College of the Atlantic in Bar Harbor, ME attracted 93 delegates from all corners of the world, including Albania, Australia, Bulgaria, Canada, Czech Republic, France, Iran, Italy, Japan, New Caledonia, New Zealand, Portugal, Russia,

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South Africa, Spain, Sri Lanka, UK, and USA, making it one of the most truly international of the six Serpentine Ecology conferences held to date (Fig. 1). The conference was testimony to the fact that serpentine outcrops worldwide are fast becoming model habitats for studies on geology-biota relations.

The Serpentine Ecology conference series had its origins in California, a biodiversity hotspot (Mittermeier et al. 2005) harboring a spectacular serpentine flora (Kruckeberg 1984, 2006), where 15% of all plant taxa (154) listed as threatened or endangered in the state show some degree of association with serpentine soils (Safford et al. 2005). The First Conference was held in 1991 at the University of California, Davis (Baker et al. 1992). Subsequent conferences have been held in New Caledonia (1995; Jaffré et al. 1997), South Africa (1999; Balkwill 2001), Cuba (2003; Boyd et al. 2004), and Italy (2006; Chiarucci and Baker 2007), always highlighting a region with intriguing serpentine soil-biota relations. The conferences have provided an opportunity for the gathering of serpentinophiles from around the world, every 3-4 years, to share and discuss their findings related to the broad and interdisciplinary field of serpentine ecology. As with the previous five conferences, the conference in Maine once again provided a setting for serpentinophiles across many disciplines and many regions to establish profitable collaborations. The conferences always feature midand post-conference tours to regional outcrops; this year's participants visited Deer Isle, a well-botanized serpentine body in coastal Maine (Rajakaruna et al. 2009) for the mid-conference tour and the magnificent Mount



Figure 1. Participants of the 6th international conference on serpentine ecology at the College of the Atlantic, Bar Harbor, Maine.

Albert, Gaspésie Provincial Park, Québec, Canada for the post-conference tour. The highlight of the mid-conference tour was the confirmation that a fern discovered in 2004 by the primary author was *Adiantum viridimontanum* (Green Mountain Maiden Hair Fern; Pteridaceae), an allotetraploid derivative of *A. aleuticum* (Aleutian Maiden Hair Fern) and *A. pedatum* (Common Maiden Hair Fern). *Adiantum viridimontanum* was previously only recorded from a few sites in Québec and Vermont and is globally rated as "vulnerable" (G3; www.natureserve.org). Delegates who participated in the post-conference tour to Gaspésie Provincial Park, hiked past ca. 100 m of packed snow near the summit to reach the famously botanized serpentine plateau on Mount Albert (1151 m; Sirois and Grandtner 1992), where they were greeted by a herd of *Rangifer tarandus caribou* (Woodland Caribou) from the Gaspé's threatened herd.

The 51 Oral Presentations and 36 Poster Presentations at the Sixth International Conference on Serpentine Ecology were grouped under the themes of geology/soils (9 talks/3 posters), biota (16 talks/13 posters), ecology/evolution (13 talks/7 posters), physiology/genetics (6 talks/9 posters), and applied ecology (7 talks/4 posters), illustrating the multifaceted effects of unusual geologies in generating and maintaining biodiversity. Participants included botanists, zoologists, ecologists, pedologists, geologists, geochemists, molecular biologists, microbiologists, evolutionary geneticists, and conservation biologists. Attendees of the Conferences are a unique group of researchers who work across disciplines in effective collaborations to explore the fascinating relationships that exist between extreme geologies and life, from cells and whole organisms to communities and ecosystems.

In this Special Issue of *Northeastern Naturalist*, we have compiled a selection of papers from among the oral and poster presentations to provide an insight into recent advances in geoecological studies of serpentine habitats worldwide. Below, we provide a preview of select papers found in this Special Issue.

First and foremost, the conference provided a venue for several researchers to present their work on the little-known serpentine habitats of eastern North America. While there has been a resurgence of interest in recent times in serpentine geoecology of eastern North America (Rajakaruna et al. 2009), the geoecology of regional serpentine soils has been largely underexplored compared to that of western North America. Alexander (this issue) describes the geoecology of the Appalachian orogenic belt, where many of the serpentine outcrops are found, focusing on the origins and extent of regional serpentine outcrops, geologic and pedologic variation found within and among outcrops, and the geoedaphic influence on the region's vegetation. Harris and Rajakaruna (this issue) explore the concept of endemism among the region's serpentine flora, a topic that has not received much attention to date. They propose several serpentine endemic species for eastern North America. Burgess et al. (this issue) highlight the Pilot Serpentine Barrens, a serpentine outcrop in Maryland, and discuss the influence of geoedaphics on the region's woody plant communities.

As always, the unique physiology of serpentine plants, especially the ability of some serpentine taxa to hyperaccumulate Ni (>0.1% in dry leaf tissue), was further discussed during this conference. Díez-Garretas et al. (this issue) report a new Ni-hyperaccumulating plant from the Iberian Peninsula, Spain, Saxifraga gemmulosa (Saxifragaceae), adding to over 390 such plants reported from all corners of the world (Reeves and Adıgüzel 2008). Ghaderian et al. (this issue) examine patterns of Ni localization in trichomes of Alyssum inflatum (Brassicaceae), a Ni-hyperaccumulating plant endemic to serpentine soils in Iran. Boyd et al. (this issue) describe their recent studies of possible ecotypic differentiation in Streptanthus polygaloides (Brassicaceae), one of only two Ni hyperaccumulators confirmed from continental North America. They document that S. polygaloides consists of four sepal color morphs differing in their Ni accumulation. They propose additional studies to determine if these morphotypes are worthy of taxonomic subdivision.

While hyperaccumulators have attracted the attention of plant physiologists for decades, the ecological implications of hyperaccumulation are still under-explored. In the past decade or so, ecologists have begun to investigate movement of elements from soils into biological communities via hyperaccumulators, and how that may affect relationships between these plants and other organisms (herbivores, decomposers, etc.; Boyd 2007, Quinn et al. 2007). Boyd et al. (this issue) add a new relationship (epiphytism) to the list of hyperaccumulator-related studies. In a study conducted in a wet forest site on serpentine in New Caledonia, they compare the metal concentrations of bryophytic epiphytes collected from Ni hyperaccumulators with those collected from non-hyperaccumulators. They report significantly elevated Ni concentrations in those growing on hyperaccumulators, suggesting that Ni may be transferred from the host plant to at least some epiphytes.

The conference also highlighted another area of growing interest, the study of plant-fungal relations in serpentine soil. Shannon Schechter presented her recently published work (Schechter and Bruns 2008) on the relationships between plant ecotypes of *Collinsia sparsiflora* (Scrophulariaceae) and distinct arbuscular mycorrhizal fungi (AMF) assemblages, showing that serpentine and non-serpentine ecotypes of *C. sparsiflora* have distinct AMF associations. Sara Branco (University of Chicago, IL, USA) explored the role ectomycorrhizal fungi play in the performance of seedlings of *Quercus ilex* subsp. *ballota* (Fagaceae), a Mediterranean evergreen oak able to colonize adjacent serpentine and non-serpentine sites in northeastern Portugal.

Another focus of the conference was on efforts for the restoration of serpentine landscapes. Centuries of mining economically valuable minerals including asbestos and heavy metal ores of Co, Cr, Hg, and Ni have left a long legacy of drastically disturbed serpentine landscapes around the world. A prime example is in the New Idria Serpentine Mass (San Benito County, CA), home to many rare Californian endemics, including

Camissonia benitensis (Onagraceae), Fritillaria falcata (Liliaceae), Layia discoidea (Asteraceae), and Monardella antonina subsp. benitensis (Lamiaceae) (Kruckeberg 1984). O'Dell and Claassen (this issue) present the challenges and triumphs associated with revegetating disturbed areas in these serpentine barrens. They provide a working framework of concepts, including physical stabilization, substrate amendment, and plant materials selection, by which drastically disturbed serpentine substrates may be successfully re-vegetated. Favero-Longo et al. (this issue) investigate the influence of plant cover on mobilization of asbestos fibers from an abandoned mining site in Italy. Their work illustrates the importance of revegetation efforts to ameliorate the hazard posed by wind-dispersed asbestos fibers from such sites.

Several presentations from serpentine enthusiasts highlighted the need to address pressing issues in biodiversity and conservation with respect to serpentine biota. Harrison et al. (this issue) present their ongoing research on effects of climate change on California's serpentine plants, stressing that plants associated with serpentine may be more likely to go extinct under predicted climate change scenarios than their non-serpentine counterparts. Their conceptual framework for assessing the impacts of climate change on serpentine endemics parallels the recent models highlighted by Loarie et al. (2008) on the effects of climate change on California's endemic plants.

Finally, a noteworthy contribution was the research of Cardace and Hoehler (this issue) on how the serpentinization process has the potential to fuel subsurface microbial metabolisms and create microbial habitats in the cool, dark subsurface on Earth. A central application of their work is to link mineralogy and habitability to remotely target extraterrestrial microbial habitats in the ongoing search for life beyond Earth's boundaries. Little did serpentinophiles realize how their model habitat for ecological studies could be linked to extraterrestrial research!

Overall, the conference was an immense success, providing an effective stage for serpentine enthusiasts to gather and share their work on rocks, soils, plants, insects, other biota, and even extraterrestrial life associated with this unique habitat. This Special Issue of *Northeastern Naturalist* has been made possible from generous support from California Native Plant Society, USDA Forest Service (Pacific Southwest Region), Missouri Botanical Garden, Maryland Native Plant Society, Maine Space Grant Consortium, Barrick Gold of North America, College of the Atlantic (Bar Harbor, ME), and several private donors from Mount Desert Island, ME. The proceeding papers highlight the status of inter-disciplinary research in the field of serpentine ecology and should generate much interest for serpentine as a model habitat for research worldwide, especially in areas where these unusual habitats are underexplored. The next conference is scheduled for 2011 in Portugal with a post-conference tour to explore serpentines of Spain. We look forward to an even stronger global presence at the next conference.

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