

1-1-2009

# Adiantum viridimontanum, Aspidotis densa, Minuartia marcescens, and Symphyotrichum rhiannon: Additional Serpentine Endemics from Eastern North America

T B. Harris

*University of Massachusetts - Amherst*

N Rajakaruna

*San Jose State University, nrajakaruna@gmail.com*

Follow this and additional works at: [http://scholarworks.sjsu.edu/biol\\_pub](http://scholarworks.sjsu.edu/biol_pub)

 Part of the [Plant Biology Commons](#)

---

## Recommended Citation

T B. Harris and N Rajakaruna. "Adiantum viridimontanum, Aspidotis densa, Minuartia marcescens, and Symphyotrichum rhiannon: Additional Serpentine Endemics from Eastern North America" *Northeastern Naturalist* (2009): 111-120. DOI: 10.1656/045.016.0509

This Article is brought to you for free and open access by the Biological Sciences at SJSU ScholarWorks. It has been accepted for inclusion in Faculty Publications by an authorized administrator of SJSU ScholarWorks. For more information, please contact [scholarworks@sjsu.edu](mailto:scholarworks@sjsu.edu).

## ***Adiantum viridimontanum*, *Aspidotis densa*, *Minuartia marcescens*, and *Symphyotrichum rhiannon*: Additional Serpentine Endemics from Eastern North America**

Tanner Harris<sup>1</sup> and Nishanta Rajakaruna<sup>2,3,\*</sup>

**Abstract** - Serpentine outcrops around the world are known to harbor disproportionately high rates of plant endemism. Remarkable cases of serpentine endemism occur in New Caledonia and Cuba, with 3178 and 920 endemic taxa, respectively, found solely on serpentine. Despite the patchy occurrence of serpentine in eastern North America from Québec and Newfoundland south to Alabama, only one taxon, *Cerastium velutinum* var. *villosissimum*, has been broadly recognized as a serpentine endemic for the region. Based on reports in the literature, we suggest that *Adiantum viridimontanum*, *Minuartia marcescens*, and *Symphyotrichum rhiannon* be considered endemic to serpentine soils from the east coast of North America. *Aspidotis densa*, with several disjunct populations on and off serpentine in western North America, is known solely from serpentine soils where it occurs in eastern North America and should be considered endemic to the substrate there. The geobotany of eastern North America in general is poorly understood, and additional taxonomic studies on the region's unique geologic substrates will likely yield further edaphic endemics.

### **Introduction**

Narrow endemism can result from any number of biological and environmental interactions. However, within a regional climate, geological discontinuities, both topographic and geochemical, are the most common and striking influences of narrow endemism (Kruckeberg 1986, Kruckeberg and Rabinowitz 1985). Among the endemic species resulting from geological discontinuities are edaphic endemics, those species restricted to chemically and/or physically unique soils (Rajakaruna and Boyd 2008). Edaphic endemics are often either products of recent *in situ* evolution resulting from divergence following colonization of a new substrate (i.e., neoendemics; Baldwin 2005, Ramsey et al. 2008) or are relicts that have experienced a reduction in their geographic or ecological ranges as a result of altered climatic or biotic conditions (i.e., paleoendemics; Kruckeberg 1986, Raven and Axelrod 1978). Recent investigations of edaphically restricted taxa provide compelling evidence in support of both modes of origin for edaphically endemic taxa (Gottlieb 2004, Mayer and Soltis 1994, Mayer et al. 1994, Pepper and Norwood 2001).

<sup>1</sup>Department of Plant, Soil, and Insect Sciences, University of Massachusetts, Fernald Hall, 270 Stockbridge Road, Amherst, MA 01003. <sup>2</sup>College of the Atlantic, 105 Eden Street, Bar Harbor, ME 04609. <sup>3</sup>Current address: Department of Biological Sciences, San José State University, One Washington Square, San José, CA 95192-0100. \*Corresponding author - Nishanta.Rajakaruna@sjsu.edu.

Serpentine soils, with their low Ca:Mg ratios, high levels of heavy metals, and generally low levels of essential nutrients, are known to harbor disproportionately high numbers of edaphic endemics compared to regional floras (Alexander et al. 2007). The tropical islands of New Caledonia and Cuba provide remarkable cases of serpentine endemism with 3178 and 920 cases, respectively (Borhidi 1992, Jaffré 1992). California alone, in western North America, is home to 176 species endemic to serpentine (Safford et al. 2005), 12.5% of the total taxa endemic to that state (Hickman 1993).

Although serpentine occurs in patches along the Appalachian orogen from Québec and Newfoundland south to Georgia and Alabama, little is known about plant life on serpentine in eastern North America compared to serpentine floras from other regions (Rajakaruna et al. 2009). Only one taxon, *Cerastium velutinum* Rafinesque var. *villosissimum* (Pennell) J.K. Morton (Caryophyllaceae; syn. *C. arvense* var. *villosissimum* Pennell) (Octoraro Creek Chickweed), has been broadly recognized as a serpentine endemic in eastern North America (Gustafson et al. 2003, Morton 2004). A second taxon once considered endemic to serpentine, *Symphyotrichum depauperatum* (Fernald) G.L. Nesom (Asteraceae) (Serpentine Aster) has subsequently been discovered on mafic diabase glades in North Carolina (Gustafson and Latham 2005, Hart 1990, Levy and Wilbur 1990). Thus, *S. depauperatum* may be considered a serpentine indicator (*sensu* Kruckeberg 1984) in eastern North America, but is not endemic to this substrate.

In a comprehensive review of the serpentine literature for eastern North America (Rajakaruna et al. 2009), we identified three additional taxa largely, if not entirely, restricted to serpentine in the region: *Adiantum viridimontanum* Paris (Pteridaceae) (Green Mountain Maidenhair Fern), *Aspidotis densa* (Brackenridge in Wilkes) Lellinger (Pteridaceae) (Indian's Dream), and *Minuartia marcescens* (Fernald) House (Caryophyllaceae) (Serpentine Stitchwort). Subsequent to our review, a fourth taxon, *Symphyotrichum rhiannon* Weakley and Govus (Asteraceae) (Rhiannon's Aster), was brought to our attention. It is a recently described species known only from the Buck Creek serpentine barrens of North Carolina (Kauffman et al. 2004). Here we make suggestions on the endemism status of all four species and discuss the status of our knowledge of serpentine endemics in eastern North America.

### ***Adiantum viridimontanum* Paris (Pteridaceae)**

*Adiantum viridimontanum* is an allotetraploid hybrid of *A. aleuticum* (Ruprecht) Paris (Aleutian Maidenhair Fern) and *A. pedatum* Linnaeus (Northern Maidenhair Fern) (Paris 1991). Of the proposed serpentine endemics in eastern North America, this species has received the most attention (e.g., O'Connor 1995, Paris 1991, Paris and Windham 1988, Ruesink 2001).

The species has been verified only from serpentine soils in Vermont and Québec (Paris 1991, Ruesink 2001, Tyndall and Hull 1999). In Vermont, it is known from 7 locations in the northern part of the state, with population

sizes ranging from 25–1000 individuals (Ruesink 2001). The species occurs at 14 sites in Québec between the Québec/Vermont border and the Thetford Mines area. We were unable to obtain specific information for the Québec occurrences. In total, it is thought that there are approximately 2000 individuals of this species in existence ([www.centerforplantconservation.org](http://www.centerforplantconservation.org)).

A possible additional station for *A. viridimontanum* was confirmed on Deer Isle, Hancock County, ME in June 2008. Based on observations of morphological features made by Arthur Haines (New England Wild Flower Society, Framingham, MA) and Geoffrey Hall (Appalachian Corridor Appalachien, Lac-Brome, PQ, Canada) and its occurrence on serpentine, it was determined that the specimens, discovered in 2004 by the senior author, were likely *A. viridimontanum*. However, a final determination cannot be made until spores have been examined.

Because *A. viridimontanum* has only recently been described (Paris 1991), it is likely that a reexamination of many of the documented serpentine occurrences of *A. pedatum* and, in particular, *A. aleuticum* (e.g., those cited by Reed 1986), will yield new localities for *A. viridimontanum* (G. Hall, pers. comm.). The possibility for further unknown occurrences of *A. viridimontanum* is also supported by the presence of primary diploid hybrids in populations of *A. pedatum* and *A. aleuticum*, suggesting the possibility for repeated origins of *A. viridimontanum* (Ruesink 2001). Repeated origins via polyploidy and hybridization are not uncommon in ferns (Shinohara et al. 2006, Treweek et al. 2002, Vogel et al. 1998).

***Aspidotis densa* (Brackenridge in Wilkes) Lellinger (Pteridaceae) Syn. *Cheilanthes siliquosa* Maxon, *Cryptogamma densa* (Brackenridge) Diels, *Onychium densum* Brackenridge, *Pellaea densa* (Brackenridge) Hooker**

In western North America, *Aspidotis densa* is known as a “faithful indicator” of serpentine (Kruckeberg 1979) ranging from British Columbia south to California and east to Montana, Wyoming, and Utah ([www.natureserve.org](http://www.natureserve.org)). In eastern North America, it is known exclusively from serpentine sites in the Mt. Albert and Thetford Mines region of Québec, Canada (Bouchard et al. 1983, Brooks 1987, Reed 1986, Tyndall and Hull 1999). In these two areas, there are seven known occurrences, each with less than 100 individuals (Thériault 1999). Three of these sites occur in protected areas, and two sites are threatened by mining ([www.mddep.gouv.qc.ca](http://www.mddep.gouv.qc.ca)). Although some work has been done on gender expression in gametophytes of this species (Greer 1993), we were unable to locate any conservation-relevant studies on its biology or ecology. Thériault (1999) produced an unpublished technical report on the species for the government of Québec; however, it has never been circulated.

Given *A. densa*'s disjunct distribution between eastern and western North America, the taxon provides a unique subject for biogeographic investigations. It is possible that the taxon dispersed from serpentine outcrops in western North America where it is more abundant and subsequently spread

among outcrops in eastern North America. Alternatively, the taxon may have had a more extensive range on and off of serpentine across the continent but is now restricted to serpentine in eastern North America, populations off serpentine having been eradicated due to unfavorable changes in climatic or biotic factors. While the first scenario implies long-distance dispersal, the latter scenario would suggest vicariance (Perrie and Brownsey 2007, Wolf et al. 2001).

***Minuartia marcescens* (Fernald) House (Caryophyllaceae) Syn. *Arenaria laricifolia* var. *marcescens* (Fernald) Boivin, *A. marcescens* Fernald**

*Minuartia marcescens* is known from ultramafic ledges and barrens in Newfoundland and Québec, Canada, and Vermont (Brooks 1987; Cook 1959; Dearden 1979; Roberts 1980, 1992; Tyndall and Hull 1999; Zika and Dann 1985). There are 20–30 occurrences totaling 20,000–50,000 individuals in Gros Morne National Park, Newfoundland. There are only two known occurrences on Mt. Albert in Québec (Reed 1986), for which we were unable to find any specific data on population size. In Vermont, there is only one known occurrence, with approximately 100 individuals ([www.natureserve.org](http://www.natureserve.org)).

***Symphyotrichum rhiannon* Weakley and Govus (Asteraceae)**

*Symphyotrichum rhiannon* was described in 2004 (Kauffman et al. 2004), ending over two decades of confusion about this species. It is thought to have been first collected and studied by Mansberg (1981), who ultimately labeled it as “unidentifiable aster” (Kauffman et al. 2004). Kauffman et al. (2004) suggested the taxon is not a recent or stabilized F1 hybrid, noting that it does not appear to be morphologically intermediate to any two species of *Symphyotrichum*. Although common garden or hybridization studies have not been performed, they note that no intergrades have been found between *S. rhiannon* and what they believe is its closest relative, *S. puniceum* (Linnaeus) Á. Löve & D. Löve (Purplestem Aster), despite the geographic range of *S. rhiannon* being imbedded within that of *S. puniceum*. If *S. rhiannon* was the product of a recent hybridization, one would expect to find morphological intergrades within its geographic range.

## Discussion

We suggest that *A. viridimontanum*, *M. marcescens*, and *S. rhiannon* be considered serpentine endemics, *sensu stricto*, from eastern North America. *Aspidotis densa* should be considered endemic to serpentine only within eastern North America as it occurs both on and off serpentine in western North America. Including *C. velutinum* var. *villosissimum*, the total of number of known serpentine endemics in eastern North America increases to five, in stark contrast to the 176 serpentine endemics that have been identified in western North America (Safford et al. 2005) and even higher numbers in other serpentine regions of the world.

The limited number of serpentine endemics in eastern North America may be due to unique ecological and evolutionary factors, including the smaller area and disjunct distribution of serpentine there relative to western North America. However, the limited number of identified endemics also likely stems from a poor understanding of the flora (Rajakaruna et al. 2009). The flora of northeastern North America was extensively studied during the 1800s and early 1900s (Fernald 1924). However, our knowledge of the southeastern flora is more limited (A. Weakley, University of North Carolina Herbarium, Chapel Hill, NC, pers. comm.). In addition, comparatively little taxonomic work has been done in eastern North America as a whole since the development of modern phylogenetic techniques.

The issue of edaphic endemism is further complicated by the possibility of edaphic races or ecotypes adapted to unique geologic substrates that may not have recognized taxonomic standing. Despite the presence of a few genera in eastern North America with known serpentine ecotypes in other regions (Brooks 1987, O'Dell and Claassen 2006), few studies have examined ecotypic differentiation in eastern North America (Rajakaruna et al. 2009). Although the taxonomic standing of such ecotypes can be a matter of contention, they clearly set the stage for speciation (Abbott and Comes 2007, Levin 1993, Rajakaruna 2004), and as such are worthy of closer study.

Despite the possibility for unrecognized edaphic races or ecotypes, the number of serpentine endemic species in eastern North America is negligible compared to serpentine regions in other parts of the world. Harrison et al. (2004) have attributed patterns of serpentine endemism in western North America to the age of exposure and outcrop size in addition to factors of climate and topography. These factors all likely play a role in the low rates of endemism for eastern North America; the serpentine areas of eastern Canada and New England were glaciated as recently as 10,000–13,000 years ago and are small in size compared to serpentine areas in western North America (Rajakaruna et al. 2009). Further, the serpentine soils in recently glaciated regions of northeastern North America are often diluted by glacial till which may ameliorate some of those aspects of serpentine soils detrimental to plant growth.

However, it is interesting to note that, with the exception of *C. velutinum* var. *villosissimum*, which occurs on the serpentine barrens of Pennsylvania (Gustafson et al. 2003, Morton 2004), and *S. rhiannon* from North Carolina, three of the five serpentine endemics in eastern North America occur in the more recently glaciated, northern latitudes of the serpentine belt. This distribution is in contrast to patterns of general endemism in eastern North America, with a greater number of endemic species concentrated in the south (Loehle 2006). The prevalence of serpentine endemics in the northern, more recently glaciated latitudes may be attributable to the greater area of serpentine in Québec and Newfoundland than in the southern regions of eastern North America (Rajakaruna et al. 2009), as would be predicted by the theory of island biogeography (MacArthur and Wilson 2001) applied to the widely accepted view of serpentine outcrops as ecological islands (Harrison et al. 2006).

A number of authors have put forth possible explanations for the evolution and maintenance of narrow endemism (e.g., Kolb et al. 2006, Lesica et al. 2006, Poot and Lambers 2008); however, there has been little agreement. As Drury (1980) and Stebbins (1980) have both suggested, there is likely no single factor responsible for such forms of rarity. Thus, studies to elucidate the influences of narrow endemism, including serpentine endemism, must be done on a species-by-species basis and must incorporate aspects of the local environment, genetic structure, and the history of both the population and the particular site. Such studies are critical to the conservation of these rare species.

In support of species-specific ecological research, García (2008) found no significant population size-extinction risk relationship for narrow endemics, suggesting that habitat preservation, as it relates to population size, may not be sufficient for the long-term persistence of such species. Thus species-specific ecological research may be necessary to determine appropriate management strategies beyond habitat preservation.

That is not to say land preservation is not a key component of any conservation plan. The serpentine barrens of Pennsylvania and Maryland, once covering nearly 20,234 ha (50,000 acres) but now reduced to a mere 1012 ha (2500 acres) (Kruckeberg 2004), serve as a reminder of the importance of land conservation. Without such basic land preservation efforts, rare species found in these unique habitats have little chance of survival. With their extirpation, we stand to lose not only potentially critical biodiversity but also the opportunity to understand important aspects of ecology and evolution (Kruckeberg 2004, Kruckeberg and Rabinowitz 1985, Stebbins 1980, Whiting et al. 2004).

### Acknowledgments

The authors thank two anonymous reviewers for useful comments, Alan Weakley for comments on *S. rhiannon*, Joe Pollard for bringing the species to our attention, Arthur Haines and Geoffrey Hall for their observations and comments on *A. viridimontanum*, and of course the attendees of the SICSE for their enthusiasm and support—one could not hope to be part of a finer scientific community.

### Literature Cited

- Abbott, R.J., and H.P. Comes. 2007. Blowin' in the wind—the transition from ecotype to species. *New Phytologist* 175:197–200.
- Alexander, E.B., R.G. Coleman, T. Keeler-Wolf, and S. Harrison. 2007. *Serpentine Geocology of Western North America*. Oxford University Press, New York, NY, USA. 512 pp.
- Baldwin, B.G. 2005. Origin of the serpentine-endemic herb *Layia discoidea* from the widespread *L. glandulosa* (Compositae). *Evolution* 59:2473–2479.
- Borhidi, A. 1992. The serpentine flora and vegetation of Cuba. Pp. 83–95, *In* A.J.M. Baker, J. Proctor, and R.D. Reeves (Eds.). *The Vegetation of Ultramafic (Serpentine) Soils: Proceedings of the First International Conference on Serpentine Ecology*. Intercept Ltd., Andover, Hampshire, UK. 480 pp.

- Bouchard, A., D. Barabe, M. Dumais, and S. Hay. 1983. The rare vascular plants of Quebec. *Syllogeus* 48:5–75.
- Brooks, R.R. 1987. *Serpentine and its Vegetation: A Multidisciplinary Approach*. Dioscorides Press, Portland, OR, USA. 454 pp.
- Cook, P.H. 1959. Discovery of *Arenaria marcescens* in the United States. *Rhodora* 61:123–124.
- Dearden, P. 1979. Some factors influencing the composition and location of plant communities on a serpentine bedrock in western Newfoundland. *Journal of Biogeography* 6:93–104.
- Drury, W.H. 1980. Rare species of plants. *Rhodora* 82:3–48.
- Fernald, M.L. 1924. Isolation and endemism in northeastern America and their relation to the age-and-area hypothesis. *American Journal of Botany* 11:558–572.
- García, M.B. 2008. Life history and population-size variability in a relict plant. Different routes towards long-term persistence. *Diversity and Distributions* 14:106–113.
- Gottlieb, L.D. 2004. Rethinking classic examples of recent speciation in plants. *New Phytologist* 161:71–82.
- Greer, G.K. 1993. The influence of soil topography and spore-rain density on gender expression in gametophyte populations of the homosporous fern *Aspidotis densa*. *American Fern Journal* 83:54–59.
- Gustafson, D.J., and R.E. Latham. 2005. Is the serpentine aster, *Symphyotrichum depauperatum* (Fern.) Nesom, a valid species and actually endemic to eastern serpentine barrens? *Biodiversity and Conservation* 14:1445–1452.
- Gustafson, D.J., G. Romano, R.E. Latham, and J.K. Morton. 2003. Amplified fragment length polymorphism analysis of genetic relationships among the serpentine barrens endemic *Cerastium velutinum* Rafinesque var. *villosissimum* Pennell (Caryophyllaceae) and closely related *Cerastium* species. *Bulletin of the Torrey Botanical Club* 130:218–223.
- Hart, R. 1990. *Aster depauperatus*: A Midwestern migrant on eastern serpentine barrens? *Bartonia* 56:23–28.
- Harrison, S., H.D. Safford, and J. Wakabayashi. 2004. Does the age of exposure of serpentine explain variation in endemic plant diversity in California? *International Geology Review* 46:235–242.
- Harrison, S., H.D. Safford, J.B. Grace, J.H. Viers, and K.F. Davies. 2006. Regional and local species richness in an insular environment: Serpentine plants in California. *Ecological Monographs* 76:41–56.
- Hickman, J.C. (Ed.). 1993. *The Jepson Manual*. University of California Press, Berkeley, CA, USA. 1399 pp.
- Jaffré, T. 1992. Floristic and ecological diversity of the vegetation on ultramafic rocks in New Caledonia. Pp. 101–108, *In* A.J.M. Baker, J. Proctor, and R.D. Reeves (Eds.). *The Vegetation of Ultramafic (Serpentine) Soils*. Intercept Ltd., Andover, Hampshire, UK. 480 pp.
- Kauffman, G.L., G.L. Nesom, A.S. Weakley, T.E. Govus, and L.M. Cotterman. 2004. A new species of *Sympyotrichum* (Asteraceae: Astereae) from a serpentine barren in western North Carolina. *SIDA* 21:827–839.
- Kolb, A., R. Barsch, and M. Diekmann. 2006. Determinants of local abundance and range size in forest vascular plants. *Global Ecology and Biogeography* 15:237–247.
- Kruckeberg, A.R. 1979. Plants that grow on serpentine: A hard life. *Davidsonia* 10:21–29.



- Kruckeberg, A.R. 1984. California Serpentine: Flora, Vegetation, Geology, Soils and Management Problems. University of California Press, Berkeley, CA, USA. 180 pp.
- Kruckeberg, A.R. 1986. An essay: The stimulus of unusual geologies for plant speciation. *Systematic Botany* 11:455–463.
- Kruckeberg, A.R. 2004. The status of conservation of ultramafic sites in the USA and Canada. Pp. 311–314, *In* R.S. Boyd, A.J.M. Baker, and J. Proctor (Eds.). *Ultramafic Rocks: Their Soils, Vegetation, and Fauna*. Science Reviews 2000 Ltd., St Albans, Herts, UK. 480 pp.
- Kruckeberg, A.R., and D. Rabinowitz. 1985. Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics* 16:447–479.
- Lesica, P., R. Yurkewycz, and E.E. Crone. 2006. Rare plants are common where you find them. *American Journal of Botany* 93:454–459.
- Levin, D.A. 1993. Local speciation in plants: The rule not the exception. *Systematic Botany* 18:197–208.
- Levy, F., and R.L. Wilbur. 1990. Disjunct populations of the alleged serpentine endemic, *Aster depauperatus* (Porter) Fern., on diabase glades in North Carolina. *Rhodora* 92:17–21.
- Loehle, C. 2006. Endemic plant distributions in eastern North America: Implications for conservation. *Journal of Forestry* 104:415–418.
- MacArthur, R., and E.O. Wilson. 2001. *Theory of Island Biogeography*. Princeton Landmarks in Biology. Princeton University Press, Princeton, NJ, USA. 224 pp.
- Mansberg, L. 1981. Vegetation, soils, and canopy age-structure of the Buck Creek Serpentine Pine Barren, Clay County, North Carolina. M.Sc. Thesis. Curriculum in Ecology, North Carolina State University, Raleigh, NC.
- Mayer, M.S., and P.S. Soltis. 1994. The evolution of serpentine endemics: A cpDNA phylogeny of *Streptanthus glandulosus* complex (Cruciferae). *Systematic Botany* 19:557–574.
- Mayer, M.S., P.S. Soltis, and D.E. Soltis. 1994. The evolution of the *Streptanthus glandulosus* complex (Cruciferae): Genetic divergence and gene flow in serpentine endemics. *American Journal of Botany* 81:1288–1299.
- Morton, J.K. 2004. New combinations in North American Caryophyllaceae. *SIDA* 21:887–888.
- O'Connor, K. 1995. Geography and ecology of *Adiantum viridimontanum*, a rare fern species in Vermont. Undergraduate Research Thesis. Department of Botany, University of Vermont, Burlington, VT.
- O'Dell, R.E., and V.P. Claassen. 2006. Serpentine and non-serpentine *Achillea millefolium* accessions differ in serpentine substrate tolerance and response to organic and inorganic amendments. *Plant Soil* 279:253–269.
- Paris, C.A. 1991. *Adiantum viridimontanum*, a new maidenhair fern in eastern North America. *Rhodora* 93:105–122.
- Paris, C.A., and M.D. Windham. 1988. A biosystematic investigation of the *Adiantum pedatum* complex in eastern North America. *Systematic Botany* 13:240–255.
- Pepper, A.E., and L.E. Norwood. 2001. Evolution of *Caulanthus amplexicaulus* var. *barbarae* (Brassicaceae), a rare serpentine endemic plant: A molecular phylogenetic perspective. *American Journal of Botany* 88:1479–1489.
- Perrie, L., and P. Brownsey. 2007. Molecular evidence for long-distance dispersal in the New Zealand pteridophyte flora. *Journal of Biogeography* 12:2028–2038.

- Poot, P., and H. Lambers. 2008. Shallow-soil endemics: Adaptive advantages and constraints of a specialized root-system morphology. *New Phytologist* 178:371–381.
- Rajakaruna, N. 2004. The edaphic factor in the origin of plant species. *International Geology Review* 46:471–478.
- Rajakaruna, N., and R.S. Boyd. 2008. The edaphic factor. Pp. 1201–1207, *In* S.E. Jorgensen and B. Fath (Eds.). *The Encyclopedia of Ecology*. Volume 2. Elsevier, Oxford, UK. 3120 pp.
- Rajakaruna, N., T.B. Harris, and E.B. Alexander. 2009. Serpentine geoecology of eastern North America: A Review. *Rhodora* 111:21–108.
- Ramsey, J., A. Robertson, and B.C. Husband. 2008. Rapid adaptive divergence in New World *Achillea*, an autopolyploid complex of ecological races. *Evolution* 62:639–653.
- Raven, P.H., and D.I. Axelrod. 1978. Origin and relationships of the California flora. *University of California Publications in Botany* 72:1–134.
- Reed, C.F. 1986. Floras of the Serpentinite Formations in Eastern North America with Descriptions of Geomorphology and Mineralogy of the Formations. Contributions of the Reed Herbarium No. 30. Reed Herbarium, Baltimore, MD, USA. 858 pp.
- Roberts, B.A. 1980. Some chemical and physical properties of serpentine soils from western Newfoundland. *Canadian Journal of Soil Science* 60:231–240.
- Roberts, B.A. 1992. Ecology of serpentinized areas, Newfoundland, Canada. Pp. 75–113, *In* B.A. Roberts and J. Proctor (Eds.). *The Ecology of Areas with Serpentinized Rocks: A World View*. Kluwer, Dordrecht, The Netherlands. 440 pp.
- Ruesink, A. 2001. *Adiantum viridimontanum* Paris (Green Mountain Maiden-hair Fern) conservation and research plan. New England Wildflower Society, Framingham, MA. 13 pp.
- Safford, H.D., J.H. Viers, and S.P. Harrison. 2005. Serpentine endemism in the California flora: A database of serpentine affinity. *Madroño* 52:222–257.
- Shinohara, W., T.W. Hsu, S.J. Moore, and N. Murakami. 2006. Genetic analysis of the newly found diploid cytotype of *Deparia petersenii* (Woodsiaaceae: Pteridophyta): Evidence for multiple origins of the tetraploid. *International Journal of Plant Sciences* 167:299–309.
- Stebbins, G.L. 1980. Rarity of plant species: A synthetic viewpoint. *Rhodora* 82:77–86.
- Thériault, A. 1999. La Situation de l'Aspidote Touffue (*Aspidotis densa*) au Québec. Gouvernement du Québec, Ministère de l'Environnement, Direction de la Conservation et du Patrimoine Écologique, Québec, Canada. 38 pp.
- Trewick, S. A., M. Morgan-Richards, S.J. Russell, S. Henderson, F.J. Rumsey, I. Pintér, J. A. Barrett, M. Gibby, and J.C. Vogel. 2002. Polyploidy, phylogeography, and Pleistocene refugia of the rockfern *Asplenium ceterach*: Evidence from chloroplast DNA. *Molecular Ecology* 11:2003–2012.
- Tyndall, R.W., and J.C. Hull. 1999. Vegetation, flora, and plant physiological ecology of serpentine barrens of eastern North America. Pp. 67–82, *In* R.C. Anderson, J.S. Fralish, and J.M. Baskin (Eds.). *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*. Cambridge University Press, New York, NY, USA. 484 pp.

- Vogel, J.C., F.J. Rumsey, J.J. Schneller, S.J. Russell, J.S. Holmes, J.A. Barrett, and M. Gibby. 1998. The origin, status and distribution of *Asplenium presolanense* spec. nov. (Aspleniaceae, Pteridophyta). *Botanica Helvetica* 108:269–288.
- Whiting, S.N., R.D. Reeves, D. Richards, M.S. Johnson, J.A. Cooke, F. Malaisse, A. Paton, J.A.C. Smith, J.S. Angle, R.L. Chaney, R. Ginocchio, T. Jaffre, R. Johns, T. McIntyre, O.W. Purvis, D.E. Salt, H. Schat, F.J. Zhao, and A.J.M. Baker. 2004. Research priorities for conservation of metallophyte biodiversity and their potential for restoration and site remediation. *Restoration Ecology* 12:106–116.
- Wolf, P.G., H. Schneider, and T.A. Ranker. 2001. Geographic distributions of homosporous ferns: Does dispersal obscure evidence of vicariance? *Journal of Biogeography* 28:263–270.
- Zika, P.F., and K.T. Dann. 1985. Rare plants on ultramafic soils in Vermont. *Rhodora* 87:293–304.