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The Serpentine Barrens of Temperate Eastern North America: Critical Issues in the Management of Rare Species and Communities

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Startlingly out of place in a forested and farmed landscape, a few patches of native prairie and savanna in southeastern Pennsylvania and northcentral Maryland attracted the curiosity of early naturalists. They named them serpentine barrens. Further exploration of the continent revealed that the native eastern grasslands resemble misplaced bits of the American West. The largest and best remaining examples now lie only a few miles from major metropolitan centers but few outside a handful of botanists, ecologists and neighboring residents know of their existence.

Serpentine barrens are best known to botanists as hotspots for disjunct and endemic plant species. These exceptional ecosystems are ranked high in priority for biodiversity conservation because they are rich in rare species of both plants and animals, including several that are globally rare and in danger of extinction. The barrens rate high in importance also because they comprise one of the rarest and most unusual sets of natural communities in the eastern North American temperate forest region.

Effective biodiversity conservation requires a thorough understanding of ecosystems, communities, and key species such as those in danger of extinction. Despite sporadic attention to serpentine vegetation by scientists, our understanding of its unusual properties remains far from complete. Nonetheless, we have a set of working hypotheses about how serpentine barrens communities work, how they are affected by human activity, and what needs to be done to insure their continued well being. This presentation is a summary of those hypotheses, including a brief review of the natural history of the serpentine barrens of temperate eastern North America.

SERPENTINE BARRENS CHARACTERISTICS

GEOLOGY. Farmers attempting to cultivate areas of serpentine vegetation called the land barren on learning that the thin soils were unproductive of crops and pasturage. *Serpentine* is the name of the rock type underlying the barrens.

The origin of the name serpentine is commonly attributed to the long, sometimes wiggly veins of minerals seen in some serpentine rocks. An alternative etymology points to ancient Italy. In northern and northwestern Italy lie many outcrops, similar to those of Pennsylvania and Maryland, of the mottled greenish bedrock. Around outcrops of the rock, the story goes, lives a mottled greenish snake. The match in coloration is not surprising, given the propensity for sharp-eyed birds of prey to eat snakes that do not blend in well with the colors of their surroundings. A cryptically colored snake basking on a rock is nearly invisible until it suddenly slithers away at the approach of a predator or a human observer. People assumed the snake and the rock were two different phases of the same mottled greenish substance. Since the animate phase was a serpent, they named the inanimate phase of this apparently mystical rock serpentine.

Serpentine was highly valued as a building stone in the nineteenth and early twentieth centuries in and around Philadelphia and Baltimore because of its striking light green color. Old serpentine buildings—typically churches, banks, or farm houses—still stand here and there throughout the region. Noteworthy examples of buildings made mostly of serpentine include College Hall and Logan Hall at the University of Pennsylvania, Philadelphia, and the coincidentally named Green Library at West Chester University, West Chester, PA.

Geologists call the rock serpentinite and the most abundant constituent minerals, serpentines. Serpentine minerals are hydrated magnesium silicates, mainly chrysotile (the most common form of asbestos) and lizardite. Serpentinites include variable quantities of other minerals, commonly including olivine, magnetite, chromite, talc and iron oxides (Pearre and Heyl 1960).

Serpentine minerals are formed beneath the ocean floor at fracture zones—areas riddled with giant cracks from stresses created by the movement of oceanic crustal plates (Saleeby 1984). Seawater leaking into deep cracks in the ocean's foundations reacts with the minerals olivine and pyroxene, constituents of the common oceanic crustal rock peridotite. The hydration of olivine-rich igneous rock is a type of metamorphism called serpentinization. Serpentinized peridotites are termed ultramafic—the "ma" for magnesium and the "f" for *ferrum,* Latin for iron—because magnesium is the most abundant metallic constituent followed by iron.

Magnesium's abundance in serpentine minerals and this metal's strong reactivity with certain acids explains why buildings clad in serpentine stone are particularly susceptible to damage in urban centers. There, smoke and car exhaust enrich the air with carbon dioxide which combines with fog and rain to form carbonic acid. The acid reacts with the stone to form highly soluble magnesium carbonate. The problem is severe in Philadelphia: crumbling serpentine walls at the University of Pennsylvania are routinely patched with green-dyed concrete.

If serpentinization occurs in oceanic crust, it follows that most serpentine rock must remain beneath the bottom of the ocean or disappear into the earth's interior in deep ocean trenches where the heavier ocean floor dives (subducts) beneath lighter continental crust. However, in a process that is still debated among geologists, slivers of serpentinite "pop up," most likely between continents moving toward each other just before they collide (Saleeby 1984). Serpentinite is far less dense than other oceanic rock and less dense than many continental rock types because serpentinization adds oxygen and hydrogen to the mineral structure. Serpentinite formations are buoyant relative to other rocks and float upward during the ponderously slow but violent process of continental collision. They are further boosted by the uplift of mountains which occurs along the sutures between colliding continents. The upward thrust of serpentinite coupled with the rapid surface erosion associated with mountain ranges eventually bring some serpentine rock to the surface.

Pieces of oceanic crust perched on the continents are called ophiolites—a word coined from the Greek words for snake and rock. Serpentinite's low density and tendency to float upward through other kinds of rock may be what drives the movement of ophiolites to the continental surface (Saleeby 1984). Ophiolite emplacement has been a relatively rare event in the earth's history. A true-to-scale world map of continental serpentine rock outcrops looks blank except for coastlines, at first glance. Only on close inspection does one notice widely scattered wispy streaks and specks. Every continent has a few outcrops, but nowhere does serpentinite occupy more than a fraction of one percent of any continent's surface. For example, in North America there are four extremely sparse clusters of serpentinite outcrops: Georgia to Newfoundland, Quebec to Manitoba, Guatemala to Cuba, and central California to Alaska (Irwin and Coleman 1972).

VEGETATION. Only a tiny fraction of the area of even these small outcrops bears a distinctive vegetation. Whether the vegetation overlying serpentine rock stands out as different from the surrounding plant cover depends on the mineral content of the serpentinite and on regional peculiarities of soil formation, present climate and climate history. The most extensive serpentine barrens in North America are those of California and Oregon. In temperate eastern North America, serpentine barrens range from Georgia to New York with more than 90% of the acreage lying in Pennsylvania and Maryland.

One of the first written accounts of serpentine vegetation in Pennsylvania was by John Bartram, in a letter dated 6 December 1745 to the Dutch naturalist John Frederic Gronovius: "The Loadstone [magnetite] lieth in a vein of a particular kind of stone that runs near east and west for sixty or seventy miles or more, appearing even with, or a little higher than its surface, at three, five, eight, or ten miles distance, and from ten to twenty yards broad, generally mixed with some veins of cotton [asbestos]. The earth of each side is very black, and produceth a very odd, pretty kind of Lychnis, with leaves as narrow and short as our Red Cedar, of humble growth, perennial, and so early as to flower, sometimes, while the snow is on the ground [*Minuartia michauxii* (Fern.) Farw., synonymous with *Arenaria stricta* Michx.]; also a very pretty *Alsine* [*Cerastium velutinum* Raf.?]. Hardly anything else grows here. Our people call them *Barrens*. . ." (Darlington 1849).

From the air, serpentine barrens look like islands. Most eastern serpentine barrens are surrounded by forests or farmland. The boundaries between serpentine and non-serpentine vegetation often appear as distinct as a true island's shore. Few plant species occur on both sides of these boundaries and those that do constitute an insignificant fraction of the local biomass. The vegetation boundaries in many cases mark a bedrock transition as abrupt as the boundary in the masonry of Penn's College Hall between the schist of the first story and the serpentine of the upper stories. The analogy is apt: serpentine formations in Pennsylvania and Maryland most often adjoin schist or gneiss.

The typical natural community on schist or gneiss is a mesic forest with a nearly closed canopy of deciduous forest trees. In contrast the quintessential serpentine barrens landscape is a prairie of mainly native grasses with scattered trees—usually *Pinus, Quercus,* or *Juniperus*—and exposed rock. Serpentine barrens are, quite literally, a textbook example of the influence of soil variation on vegetation structure and composition. Plant associations growing atop serpentine outcrops all over the world are cited by ecology, botany, and soil science textbooks as models of azonal vegetation, that is, vegetation resembling the norm of some other climatic zone.

Large, well developed serpentine communities are actually mosaics of different serpentine plant associations, reflecting variation in soil development, bedrock mineral content, moisture availability, successional age since the last episode of natural disturbance, and the type of disturbance (K. S. Dougherty, unpubl. ms.). The open-canopy rock exposure communities (sometimes called glades) and the grasslands are richest in disjunct, endemic and rare species. Wetlands overlying serpentine are highly minerotrophic and have a distinct flora. Several forest types also occur on serpentine including closed-canopy *Pinus rigida, Quercus stellata-Quercus marilandica* oak woods and, at one location only (in Lancaster County, PA), what appears to be a giant clone of *Populus tremuloides,* possibly a relict of periglacial climate. Serpentine forests usually have a nearly impenetrable understory of *Smilax rotundifolia* and *Smilax glauca.*

DISTRIBUTION. At the core of the eastern serpentine archipelago lie the state line barrens—a string of seven sites along 20 km of the Mason-Dixon Line in Chester and Lancaster Counties, PA, and Cecil County, MD. Six are in Pennsylvania, three extend a short distance into Maryland, and one is entirely in Maryland. Totalling approximately 850 ha, these sites comprise the largest area of serpentine vegetation in the eastern temperate zone across which serpentine-restricted plant and insect species are likely to form locally interbreeding populations. The two largest of the seven sites, Goat Hill and Nottingham Barrens, lie near the geographic center of the state line barrens. Separated by less than 2 km they encompass approximately 400 ha of serpentine vegetation, mainly savanna dominated by *Schizachyrium scoparium, Sporobolus heterolepis,* and *Pinus rigida.* Scattered glades include the only two known eastern temperate serpentine endemics: *Aster depauperatus* (Porter) Fern. (serpentine aster) and *Cerastium velutinum* Raf. (lumped with *C. arvense* L. in most floral manuals) var. *villosissimum* Pennell (long-haired barrens chickweed).

Soldiers Delight in Baltimore County, MD, a 540-ha area of serpentine vegetation 60 km southwest of the state line barrens, is the largest single eastern serpentine barrens site. Its flora is among the richest in species diversity of all the barrens but it lacks the endemics and the typical state line barrens dominants *Pinus rigida* and *Sporobolus heterolepis.*

Discounting a few very small sites (<2 ha), the remaining eastern serpentine barrens cover up to 40 ha per site and are scattered from Georgia (1 site) through North Carolina (1) and Maryland (3) to northern Chester and Delaware Counties, Pennsylvania (6), and New York (4 small sites on Staten Island). Altogether there are 23 serpentine barrens sites ≥ 2 ha in temperate eastern North America. A number of small areas of serpentine vegetation recorded historically has been destroyed by incompatible land use including nearly a dozen sites in the western suburbs of Philadelphia and one in northern Delaware.

All temperate eastern North American serpentine barrens occur on serpentine rock in the Piedmont physiographic province except for the one in North Carolina, which occurs on olivine and serpentinized dunite in the Blue Ridge province (Mansberg and Wentworth 1984).

DISJUNCT AND ENDEMIC SPECIES. Serpentine barrens form archipelagoes of specialized habitats for species with disjunct and endemic distributions. The characteristic plant species of the barrens can be classified in several ways: regional fidelity to serpentine, the region or habitat where they are most abundant off serpentine, and regional or global rarity. A few examples will illustrate.

One of the showiest characteristic serpentine species, *Phlox subulata,* is an example of a species restricted to serpentine locally within the counties with serpentine outcrops. Elsewhere it occurs on dry rock exposure communities including the Appalachian shale barrens. Pink Hill, a serpentine barren at Tyler Arboretum, Delaware County, PA, takes its name from the masses of *P. subulata* flowers that appear there in early spring during favorable years. Another showy species, *Lilium philadelphicum,* inhabits a variety of dry, relatively open sites, but is still considered a characteristic member of the serpentine flora.

A group with special biogeographical interest includes those species whose main range lies in the western plains. Their populations on serpentine are generally considered as relicts of a warmer and drier interval called the hypsithermal, which occurred from 7,000 to 2,500 years ago following the most recent glacial maximum (Deevey and Flint 1957). During the hypsithermal, these species may have been far more abundant across central and eastern North America. *Carex bicknellii, Bouteloua curtipendula,* and *Sporobolus heterolepis* fall into this category. *Asclepias verticillata*—an unusual milkweed with almost needle-like leaves—is also a western prairie disjunct.

Fimbristylis annua, with a mainly tropical and subtropical distribution, behaves as if it were a desert annual. Its soil seed bank suddenly germinates to form lush carpets of turf only in years when rainfall occurs abundantly and at the right time during the season. Pennsylvania's serpentine populations lie at the northernmost limit of the species' global range. *Senecio anonymus* Wood (*S. smallii* Britt. in most floral manuals) is another species reaching its northern limit in Pennsylvania's serpentine barrens. *Scleria pauciflora,* with fruits resembling miniature golf balls, inhabits soils and sands that are low in mineral nutrients. All three species occur almost exclusively on serpentine in southeastern Pennsylvania and northcentral Maryland and are classified as rare in both states.

Talinum teretifolium (fameflower) inhabits several types of rock outcrops throughout its highly fragmented range. As is typical of the Portulacaceae, its stems and leaves are succulent. The serpentine populations in Pennsylvania and Maryland define the northern limit of its range. They are separated by hundreds of kilometers from the next-nearest population on a granite outcrop in southern Virginia (W. H. Murdy, pers. comm.). How the species' tiny seeds found their way to nearly a dozen widely scattered serpentine outcrops in the northern Piedmont is a mystery that may keep biogeographers guessing for a long time. Dr. William Murdy of Emory University conjectures that they may have been lofted by windstorms or possibly by a single windstorm. Such a scenario requires a fortuitous combination of a tornado or other strong updraft raking across one or more southern rock outcrops, storm movement along a track intersecting the northern serpentines, and deposition on the serpentines. The absence of differences detectable by gel electrophoresis at 23 gene loci between serpentine and other populations of *T. teretifolium* suggests that the species' colonization of serpentine was relatively recent (Murdy and Carter 1985).

Among the rarest species living on the barrens are the two eastern temperate serpentine endemics. *Aster depauperatus,* with its distinctive summer-deciduous cauline leaves and winter-persistent basal rosette, is known from about a dozen sites in Pennsylvania and adjacent areas in Maryland. Recently, its endemic status was challenged by the discovery that it occurs at three diabase glades in north-central North Carolina (Levy and Wilbur 1990). *A. depauperatus* currently is regarded as a suspect taxonomic entity. Dr. Robin Hart has presented morphological evidence obtained from common-garden experiments that *A. depauperatus* may actually be an eastern disjunct of *A. parviceps,* a prairie species with a restricted range in Illinois, Iowa, and Missouri (Hart 1990).

The taxonomy of the other eastern temperate serpentine endemic is also in question. The species name *Cerastium velutinum* Raf. has recently been resurrected to refer to a hairy broad-leaved form of *C. arvense* L. (vars. *villosum* (Muhl.) Hollick & Britt, and *villosissimum* Pennell in floral manuals) restricted to serpentine and limestone glades (Morton 1987). The discovery that the distinctions of anatomy and habitat distribution parallel a different chromosome number makes a convincing case for the revival of the species split. *C. velutinum* may be a rare species in its own right. Its revival as a separate species is so recent that no one has yet tried assessing its global abundance.

Var. *villosissimum,* with distinctively long white hair covering leaves and stem, is often said to occur in only one place in the world—bluffs overlooking Octoraro Creek at Goat Hill, Chester County, PA, from which the type specimen was collected and described by Francis W. Pennell (1930). Herbarium specimens from at least three other Pennsylvania serpentine sites were labelled as var. *villosissimum* and a recent discovery, still unpublished, places var. *villosissimum* at a serpentine barren in Maryland. However, *Cerastium* monographer Dr. John Morton of the University of Waterloo considers var. *villosissimum* to be a taxonomically trivial form, based on several lines of experimental and observational evidence (J. K. Morton pers. comm.).

Adiantum pedatum subsp. *calderi* (serpentine maidenhair) is the only endemic shared between serpentine outcrops of both eastern and western North America. It is the most shade-tolerant of all the plants that have high regional fidelity to eastern serpentine outcrops, commonly occurring in the understory of serpentine woods. Recent biosystematic research (Paris and Windham 1988) suggests it may be better considered as a full species distinct from *A. pedatum*. The study also showed evidence that *calderi* is likely to be more closely related to maidenhair ferns of the western mountains than to the common maidenhair of eastern forests.[1]

Other globally rare and endangered species are also found on the barrens. The rarest may be *Agalinus acuta* (sandplain gerardia). It lives at one Maryland serpentine barren and fewer than a half dozen non-serpentine sites northward along the Atlantic coast. Another is *Elliottia racemosa* (Georgia plume), an ericaceous shrub or small tree whose entire range is confined to scattered sites on Georgia's coastal plain and to the Burke Mountain, GA, serpentine barren.

Euphorbia purpurea (glade spurge) is known to occur at less than 20 places globally including the Goat Hill, PA serpentine barren and a site in Virginia underlain by a gabbro formation considered to be mafic (ferro-magnesian but to a lesser degree than rock classed as ultramafic) and sharing some mineral characteristics with serpentine. *E. purpurea*, a wetland species, directs attention to the fact that not all serpentine habitats are dry uplands. Some groundwater-fed wetlands at serpentine outcrops have a distinctive flora, most often typified by *Deschampsia cespitosa* or *Sanguisorba canadensis*.

Not all rare species characteristic of serpentine barrens are plants. The unusual plant communities host numerous specialist-feeder insect species. As with plants, many of the serpentine populations of insects are disjunct from the species' main ranges. The buckmoth (*Hemileuca maia*) is one of the most conspicuous of the rare insect species with high regional fidelity to serpentine. Unlike most moths it flies during the day. It can be spotted in late October and early November by its distinctive black and white wing markings, large size, and rapid bouncing flight. Buckmoth larvae, spectacularly armed with stinging hairs, feed on the leaves of *Quercus ilicifolia*.

PHYSIOGNOMY. The salient fact of serpentine biogeography is the convergence of community physiognomy. Most serpentine communities look like dry prairies and savannas even where they are well watered and surrounded by lush forests. The southernmost temperate eastern North American serpentine barren—Burke Mountain, GA—is a pine-grass savanna in which *Pinus palustris* (an isolated population) and *Pinus echinata* substitute for the *Pinus rigida* of the state line barrens. More remarkably, the aspect of much more distant serpentine barrens often closely resembles the appearance of the sites in Pennsylvania and Maryland. For example, Gasquet Mountain, CA, has a pine-grass savanna dominated by *Pinus jeffreyi*, *Pinus monticola*, *Festuca idahoensis* and *Poa piperi*. The presence of savanna on serpentine may not seem remarkable in California where oak savanna is one of the most widespread natural community types. However, Gasquet Mountain stands adjacent to coastal redwood forests and the serpentine barrens there, on average, receive more than four times the annual rainfall (Goforth 1984) as those in Pennsylvania and Maryland!

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[1] A paper published after this symposium places serpentine maidenhair in *A. aleuticum* (Rhodora 93:105–121).

An amazingly large proportion of the plant life at Gasquet Mountain looks quite familiar to an eastern serpentine devotee. One is struck by the high degree of convergence in phylogeny—some higher taxa appear to be "preadapted" for life on serpentine—and in morphology—one sees similar, apparently adaptive traits across a wide phylogenetic spectrum. *Phlox adsurgens* is strongly reminiscent of *Phlox subulata, Senecio macounii* looks like *Senecio anonymus,* and the serpentine endemic *Lilium bolanderi* closely resembles *Lilium philadelphicum.* The eastern naturalist may spot a plant that looks very much like *Asclepias verticillata* and, on finding a flower, discover it to be a lavender-rayed composite instead, *Erigeron foliosus* var. *confinis.*

Despite the similarities, many species appear totally unfamiliar to an easterner. For example, the flowers of *Calochortus tolmiei* (Liliaceae) have purple anthers surrounded by large blunt white petals covered with hundreds of projections resembling tentacles. The rare *Sedum laxum* subsp. *heckneri* is a sprawling succulent with dramatic upright candelabras of large pink and white flowers. *Darlingtonia californica,* a pitcher plant, has insectivorous leaves up to 60 cm tall that look like a cross between a rearing cobra and a giant banana slug. These and many other stunningly unfamiliar plants remind the eastern naturalist that the California serpentines are far larger in area and have been less buffeted by severe climate changes during the Pliocene and Quaternary compared with those in Pennsylvania and Maryland, allowing the processes of colonization and evolution greater scope in generating diversity.

Even within the flora of the temperate eastern North American serpentine barrens, convergence in morphology across taxa is striking. For example, the basal rosette habit is well developed in species from a wide range of families. *Arabis lyrata* (Brassicaceae), *Aster depauperatus* (Asteraceae), and *Panicum sphaerocarpon* (Poaceae) all have basal rosettes that are nearly identical in diameter, height, and general aspect. *Asclepias verticillata, Phlox subulata,* and *Polygonum tenue* have linear leaves atypical of their respective families and genera. These and other morphological traits such as leaf pubescence (*Cerastium velutinum*) and succulence (*Talinum teretifolium*) are most often associated with hot or dry habitats. Although the serpentine barrens are not dry, the rocky glades inhabited by all the plants listed in this paragraph can be quite hot in summer. Infrared radiation reflected and re-radiated from bare shales, granites, limestones, serpentine, and other rock types commonly occurring with little or no soil cover may well have been the selective force favoring characteristics such as basal rosettes, linear leaves, pubescence, and succulence.

SOIL FACTORS. But why is the rock bare in the first place? In regions of high rainfall such as Pennsylvania and Maryland, what prevents weathering and biological processes from covering serpentine with a thick layer of soil and vegetation as is the case with virtually all neighboring bedrock formations? Before considering these important questions, I will address one that is more fundamental. Soil does cover the bedrock beneath the other types of serpentine vegetation besides that growing on exposed rock or glades—the serpentine prairies, savannas, woodlands, and minerotrophic wetlands. Why are these types of vegetation still quite different from nearby vegetation on soils weathered from non-serpentine bedrock?

Most explanations focus on mineral nutrient conditions in soils weathered from serpentine bedrock. Serpentine soils have exceptionally low levels of nitrogen, phosphorus, potassium, and calcium—the minerals needed by plants in greatest quantity. The soils are also exceptionally high in nickel, chromium, and cobalt—metals known to be toxic to plants in high concentrations. However, experiments conducted by manipulating these factors in ordinary soils have failed to show a consistent link between any one of them and the species-specific effects of actual serpentine soils on plant growth and survival (Proctor and Woodell 1975; Brooks 1987).

Arthur Kruckeberg's experiment (1954) with plants from serpentine and non-serpentine populations of *Phacelia californica* is one of several studies that point to the magnesium: calcium ratio as the main factor limiting plant growth on serpentine sites. Ordinary soils typically have approximately one or two exchangeable calcium ions for every exchangeable magnesium ion. In serpentine soils the ratio is dramatically reversed. A survey of 156 serpentine soil samples from four continents showed a mean of 7.5 exchangeable magnesium ions for every exchangeable calcium ion (Proctor and Woodell 1975); Mg:Ca ratios of 20–100 are common and at least one sample has exceeded 300 (Brooks 1987).

Apparently many plant species, especially plants that are capable of fast growth, are physiologically "confused" by an excess of magnesium relative to calcium. Their calcium-handling enzymes may begin to bind with magnesium under conditions of magnesium abundance combined with calcium deficiency (Proctor and Woodell 1975). Even though magnesium is an essential plant nutrient (it forms the core of the chlorophyll molecule), at high concentrations or in combination with calcium deficiency it interferes with the uptake of other minerals or acts as a toxin, or both, leading to retarded growth, disease, or death.

Little is known of the physiological mechanisms that enable certain plants to handle high magnesium:calcium ratios. Presumably some have means of preventing magnesium from substituting for calcium. For example, some plants growing on serpentine may have highly discriminating versions of the enzymes responsible for calcium uptake, calcium transport, and the assembly of calcium-bearing biochemicals.

There is a common misconception that plants apparently restricted to serpentine habitats actually require serpentine soils. To the contrary, virtually all serpentine plants grow better on ordinary soils than they do on serpentine soils in pots or gardens where potential competitors are absent. The key to this paradox is a trade-off, apparently universal in the plant kingdom, between tolerance of nutrient deficiency and maximum growth rate (Chapin 1980). Constrained by the incompatibility of key physiological and morphological traits, members of a species can be good at tolerating nutrient scarcity or other nutrient stresses such as high magnesium:calcium ratio or they can be good at growing rapidly where nutrients are abundant or normally balanced, but not both. An inherently low upper limit on growth rate apparently is a side effect of the adaptations enabling plants of some species to grow under difficult nutrient conditions (Chapin 1980). Plants that can take advantage of nutrient abundance by growing fast and quickly depriving their neighbors of sunlight usually die in situations of nutrient stress. Thus, certain plants that are tolerant of nutrient stress can achieve competitive dominance on serpentine soils despite their low growth rates. They grow somewhat faster on nonserpentine soils but not fast enough to prevent succumbing to shading and crowding by much faster-growing plants that are *in*tolerant of nutrient stress.

Other factors may be important in limiting the local distributions of some plants to serpentine sites. For example, even though one might expect plants with nitrogen-fixing root symbionts to have a competitive edge in generally high-light, low-nitrogen environments such as the serpentine barrens, very few such plants are present (exceptions on the Pennsylvania and Maryland barrens are *Cassia fasciculata* and the introduced *Robinia pseudoacacia*). Some scientists have attributed this paradox to exceptionally low concentrations of molybdenum in serpentine soils (Walker 1948; White 1967). Molybdenum is the central ion in the enzyme employed by nitrogen-fixing bacteria and actinomycetes to reduce N_2 (atmospheric nitrogen) to NH_4+ (ammonium) usable by plants.

At least one investigator has suggested that there may be exceptions to the rule that serpentine plants grow better on ordinary soils than on serpentine soils. T. M. Tadros (1957) assayed the growth responses of a serpentine-restricted species in California, *Emmenanthe rosea* (Hydrophyllaceae), to serpentine and non-serpentine soils with half of each soil type exposed to enough heat to kill all microorganisms. The plants thrived on sterilized non-serpentine soils but failed to germinate on those that were not sterilized. The scientist hypothesized from this result that the serpentine-restricted species lacks innate resistance to some fungal pathogen of seedlings but that it is protected in its native habitat by the fungus's intolerance of serpentine conditions.

The hypothesis to my knowledge remains untested but it is an appealing idea. One of the most common causes of plant mortality is damping-off—a generic term for lethal attacks upon seedlings by various fungi. If such fungi avoid serpentine soil then they are not capable of selectively favoring resistance in potential host populations growing on serpentine. It follows that plant populations living entirely on serpentine and not interbreeding with populations living off serpentine could lose resistance to fungal attack by genetic drift. In this way, hypothetically, entire plant populations could become obligate serpentine dwellers.

Conservation Threats

So far I have reviewed a number of explanations for why the vegetation of serpentine barrens is so distinct from the surrounding plant life. But none of these explanations has addressed why the soil is thin and why there is often much bare rock on the barrens. It is true that the rate of plant growth on the barrens and the resulting rate of organic matter production are slow on the barrens relative to adjacent communities. However, soil formation depends on net organic matter accumulation, a function of both production and decomposition (Olson 1963). Areas free of soil should result only if serpentine conditions impede rates of plant growth more than they impede rates of decomposition. Little evidence exists to support or refute this hypothesis. In order to establish a foundation for what I believe is a more compelling explanation, I will take a short detour from biology and focus attention on conservation issues. What are the threats to this unique ecosystem in the eastern USA?

MINING AND QUARRYING. Pennsylvania and Maryland's serpentine outcrops were the world center of chromium mining in the late nineteenth century, when the main use for chromium was as a pigment in paint. Other minerals including talc, asbestos, and corundum as well as building stone were also extracted commercially. The serpentine barrens at Gasquet Mountain, California, have been seriously threatened by a proposed large-scale nickel mining operation. Currently there is a huge active serpentine quarry in southern Lancaster County producing crushed stone for concrete and asphalt paving.

Serpentine barrens conservation in Pennsylvania began after a plea from neighbors of Goat Hill worried about a proposal to strip-mine the rock there. To date, land totalling 278 ha has been acquired for the Goat Hill serpentine barrens nature preserve by The Nature Conservancy (a private organization dedicated to conserving biological diversity by identifying the best remaining occurrences of natural communities and rare species, protecting the land, and redressing any adverse effects of human land use).

DEVELOPMENT. Northern Chester County and central Delaware Counties, PA, are littered with more than a dozen small dead and dying serpentine barrens, eaten away by housing developments, two golf courses, and other types of intensive land use. Until recently, serpentine barrens have enjoyed a modest level of natural protection: the soils are poor for growing crops and they usually fail to meet percolation requirements for septic tank construction. But newer high density developments and the gradual coalescence of the patchwork of suburban sprawl make sewer systems economically feasible. Equipped with sewers and treatment plants, serpentine barrens suddenly become developable. Riddle Hospital currently plans to build a nursing home atop one of two remaining barrens in Delaware County, which once harbored at least nine such sites. In response to protest by citizens and the Pennsylvania Department of Environmental Resources, construction plans were revised to show a set-aside—a tiny patch labelled "serpentine aster"—with recontoured ground, landscape planting, and a wing of the proposed building still occupying most of the actual serpentine barrens community. This plan exemplifies what might be termed the flower-garden approach to rare species conservation, doomed to failure. No law exists in Pennsylvania that can be invoked to protect this rare natural community or the globally rare species that lives there.

INVASION BY NON-SERPENTINE VEGETATION. The other remaining serpentine barren in Delaware County, Pink Hill, is protected from development as part of the Tyler Arboretum. But is protection from bulldozers enough? A closer look suggests otherwise. *Robinia pseudoacacia* has invaded the serpentine prairie at Pink Hill and appears to be spreading. It was introduced to the region from its pre-European settlement range in the Appalachian and Ozark mountains and the Ohio valley (Fowells 1965). Without intervention this aggressively invasive tree would doubtless cover tiny Pink Hill's entire prairie area in only a few years.

Even at Goat Hill, with a barrens area almost 100 times larger than Pink Hill, there are signs of invasion by species not considered as characteristic members of the serpentine flora. Around the fringes of the barrens, large *Pinus rigida,* many dead or dying, stand among young woods dominated by *Acer rubrum, Prunus serotina, Robinia pseudoacacia,* and *Ailanthus altissima.* An aerial view of the heart of the Goat Hill barrens reveals that the *Pinus rigida* canopy is nearly closed across most of the savanna. Prairie openings—common on other barrens of the state line group—are nearly absent at Goat Hill.

A comparison of historic and modern aerial photos reveals a dramatic pattern. An aerial photo taken at Pilot Barrens, Cecil County, MD, in 1938 shows vast areas of open prairie and sparse savanna. A photo of the same site taken in 1988 presents quite a different picture. Only one comparatively small area of prairie remains. Most of the area formerly in barrens now has closed-canopy forests of *Pinus virginiana.*

Why do the barrens appear to be declining or even disappearing in just a few decades when we can infer with confidence from the distributions of so many indicator plant species that the communities have existed for thousands of years? Searching has turned up numerous clues.

Importance of Fire in Perpetuating Barrens Communities

Charred bark is a common sight on *Pinus rigida* of serpentine savannas and glades. Trunks and limbs of many *Pinus rigida* also sport a green "fur" of adventitious shoots. It is not uncommon to see *Quercus marilandica* and *Quercus stellata* with leaves bunched tightly around a stout trunk on disproportionately small twigs, with larger branches either dead or absent. Adventitious shoots spring from epicormic buds present in these particular pine and oak species but not in other tree species living in the region. In the pine barrens of the New Jersey coastal plain and at certain other sites, these buds are most often released from dormancy by fire.

The serpentine dominant *Sporobolus heterolepis* is a bunch grass common in the shortgrass prairies of the Dakotas, Nebraska, and other parts of the West. Bunch grasses build up masses of living and dead plant tissue around their crowns. The material acts as effective insulation shielding crown meristems from the heat of prairie ground fires, which occur frequently in shortgrass country. Furthermore, seeds in the soil from this and some other prairie species reportedly break dormancy and germinate most profusely immediately following a fire.

A study conducted in the 1960's and 1970's confirmed the implications of numerous fire-adapted traits in the serpentine flora. Botanist Gary Miller undertook a vegetation distribution analysis on a serpentine barren in southern Lancaster County, PA, for his master's thesis. Fortuitously, a major wildfire swept through many of his sampling plots five years after he had collected species abundance data. In resampling six and nine years post-fire, he found increases or little change in cover by many of the characteristic serpentine species, including the addition of previously unrecorded *Aster depauperatus.* He also found substantial decreases in cover by species more commonly found on non-serpentine soils, including the virtual disapperance of formerly abundant *Pinus virginiana* (Miller 1981).

Many plant species inhabiting regions or natural communities where wildfires are common have traits enabling them to survive a fire if it is not too severe. Some of these species are even suspected to have traits that *facilitate* relatively cool, fast-burning fires (Mutch 1970; Platt, Evans and Rathbun 1988). These may include air pockets, volatile resins, resistance to absorption and retention of moisture, and other flammability-enhancing traits in cast-off leaves and other tissue. Vegetation dominated by species with such characteristics tends to ignite, especially in the dormant season, at any provocation—lightning, a discarded cigarette, a spark from burning trash or a campfire—while ordinary vegetation is likely at most merely to smolder except during severe drought. Species acting as "ecological arsonists" may have hit upon, evolutionarily, a means of eliminating competitors of fire-intolerant species.

The barren-dwelling plants have apparently undergone an evolutionary trade-off. In acquiring the abilities to tolerate infertile soil and frequent wildfire, they have sacrificed the ability to grow fast and aggressively compete for sunlight (Chapin 1980; Grime 1977). Thus, the vegetation of the serpentine barrens is fire-dependent. In the prolonged absence of fire, mesic vegetation may invade serpentine barrens producing litter that readily absorbs and retains moisture, is resistant to igniting and carrying flame, and decays to form soil rich in organic matter. The enriched soil may shift the entire system over to a different self-perpetuating community dominated by non-barren plant species (Streng and Harbcombe 1982).

Frequent wildfire would explain the presence of bare rock and thin soil, two of the key characteristics of the barrens that may be crucial to maintaining the distinctiveness of the vegetation. Fire turns carbohydrates, the largest constituent of organic matter by volume, into carbon dioxide, water vapor, and smoke. The organic matter that is so important to building soil and holding it in place against erosion is periodically lost from the system in massive quantities. Exceptionally hot fires, for example, where the wood of large trees provides abundant fuel, may burn organic matter even after it has been incorporated into soil. Thin soils and bare rock most likely result from the interaction of fire and water erosion.

FIRE SUPPRESSION. Accounts from the *Daily Local News,* a Chester County, PA, newspaper, give clues about why the serpentine barrens are shrinking. From 20 April 1908: "A forest fire is raging in the pine barrens just to the south of Oxford. . . . No effort is being made to stop the progress of the fire, it being allowed to burn itself out." From 7 May 1962: "More than 300 volunteers from 14 fire companies were called into the battle to *save the* *area,* known as the Barrens . . ." (italics are mine). Sometime between 1908 and 1962, active fire suppression came to the rural areas where eastern serpentine barrens occur.

Not all fire suppression involves pumpers and hoses. An aerial photograph of Chrome Barrens, Chester County, PA, shows a plethora of inadvertent firebreaks including the road bisecting the barrens, driveways, farm fields, pastures, and lawns. Long-time neighbors recall only one relatively small wildfire at Chrome Barrens in the past 50 years.

PRESCRIBED BURNING AS A MANAGEMENT TOOL. What can be done about this most subtle of threats to the integrity and persistence of the eastern serpentine barrens? At the state line barrens, staff of The Nature Conservancy in Pennsylvania and Maryland have embarked upon a stewardship program designed to counter the effects of decades of fire suppression and to restore periodic fire to its rightful position as an integral force in serpentine community dynamics. A similar program is underway at Soldiers Delight by the Maryland Natural Heritage Program, an agency of the state Department of Natural Resources.

The program starts with research, beginning with an assay of herbaceous and woody plant species abundances on permanently marked sampling plots. The next phase is prescribed burning, the carefully planned and controlled use of fire by trained experts under optimum conditions of wind, humidity, fuel moisture, and other critical factors. The ignition, spread and movement of the fire is tightly controlled to burn a precisely specified area. Burn units include only half of the vegetation sampling plots, allowing researchers to tease apart the effects of fire from other influences on vegetation such as insect or disease outbreaks, weather, soil nutrients and soil moisture.

Prescribed burning accomplishes several ends. It provides information critical to the long-term protection of fire-dependent systems by allowing experimental evaluation of the effects of fire on species abundances and distributions. By imitating the effects of wildfire it restores a vital component of the natural disturbance regime to communities that show evidence of decline due to fire suppression. It also reduces the natural fuel load and with it the threat of catastrophic, uncontrollable wildfire.

In some places, many tons per acre of highly flammable natural fuels have accumulated due to the artificial suppression of fire. Ironically, in a community of plants with traits conferring high flammability, fire prevention in the short term increases fire hazard in the long term. This is a lesson resource managers have learned over and over the hard way. The principle made the news after the 1988 fires at Yellowstone National Park, where decades of fire suppression had resulted in massive fuel build-up which in turn led to unusually hot and widespread fires during an ordinary episode of drought. Yellowstone covers a large enough area and is so sparsely settled that land managers have the option of allowing wildfires to burn unimpeded. In an area as densely populated as the northeastern USA, a "let it burn" wildfire policy is virtually unthinkable. Here, prescribed burning offers a practical and environmentally sound way of preventing massive fuel build-up in fire-dependent ecosystems and staving off catastrophic wildfires.

The first of many planned ecological burns at the state line barrens took place in fall, 1990, at Pilot Barrens under the direction of Conservancy biologist Mary Droege. The first burn at Chrome Barrens, to be led by Conservancy biologist Michael Batcher, and the second burn at Pilot Barrens are planned for late 1991-early 1992.

OTHER FIRE-DEPENDENT NATURAL COMMUNITIES. Serpentine barrens are not the only natural communities considered to be fire-dependent in the mid-Atlantic region of eastern North America's deciduous forest biome. New Jersey's pine barrens, especially the dwarf forests known as the Plains, are probably the most extensive and best known example. The Albany Pine Bush and Long Island's pine barrens in New York exhibit the syndrome of fire-dependency. All are sites of active prescribed burning programs conducted by state agencies, The Nature Conservancy, and other groups charged with the stewardship of natural areas.

In Pennsylvania a few small fragments of limestone glades and prairies have escaped cultivation, including communities characterized by *Dodecatheon meadia* and *Poa compressa* at Conococheague Bluffs, Franklin County, and by *Bouteloua curtipendula* at Westfall Ridge Prairie, Juniata County. The Appalachian sand barrens near Gatesburg in Centre and Huntingdon Counties and the Appalachian shale barrens of Bedford, Fulton, and Huntingdon Counties also probably have varying degrees of fire-dependence.

The Pocono till barrens in northeastern Pennsylvania are the state's most extensive fire-dependent community. They cover an area several times greater than the serpentine barrens and have similarly rich complements of rare species. The Pocono barrens lie overtop the state's largest intact deposit of Illinoisan glacial till, a remnant of the second-most recent glacial advance 140,000 years ago, in Monroe and Carbon Counties. Dominant and characteristic species of these barrens include *Pinus rigida, Quercus ilicifolia, Rhododendron canadense, Kalmia angustifolia, Vaccinium angustifolium, Oryzopsis pungens, Carex polymorpha, Carex vestita,* and *Amianthium muscaetoxicum.*

Like serpentine soils, the soils weathered from Illinoisan till on the Pocono Plateau have unusually low mineral nutrient concentrations. Like serpentine vegetation, the plant life of the Pocono till barrens is well watered but has the aspect of vegetation native to a far drier region. Like the serpentine barrens, the Pocono till barrens are prone to wildfire and many of the plants exhibit traits associated with fire dependence. The community is so distinctive that its one large and several small occurrences on the Pocono Plateau are considered to be the planet's entire inventory of the type. It is host to many rare species including the globally rare and endangered *Carex polymorpha.* At least seven globally rare and endangered insect species inhabit the Pocono barrens including the only insect species whose entire known range is confined to Pennsylvania—the flypoison bulb-borer moth (*Papaipema* sp. 1), which feeds on the highly toxic root of *Amianthium mascaetoxicum.*

CONCLUSIONS

Fire-dependent natural communities make up less than a tenth of one percent of Pennsylvania's total area, yet they include about 10% of the state's known occurrences of globally rare plants and animals (species or subspecies represented by 20 or fewer total populations) and natural communities ranked as having global significance. Unlike many southern, midwestern and western states, Pennsylvania has almost no recent tradition of using fire in farming, forestry or wildlife management. Much of what people in Pennsylvania and other northeastern states typically know about wildfire they learned from Smokey the Bear. Prescribed burning is the best way to achieve certain important research, conservation, and wildfire prevention goals but it cannot succeed without increased awareness and acceptance by government officials, neighbors of fire-dependent natural areas, and the general public. Unfortunately, the bias that all fires are tragedies permeates the public perception and is often exacerbated by the style and content of journalists' coverage (Smith 1989).

The long-term persistence of Pennsylvania's rarest and most unusual terrestrial communities depends on scientists and resource managers adopting fire as a tool of biodiversity conservation. It also depends on a convincing, well targeted campaign by knowledgeable and concerned people to spread the word about the ecological importance of fire.

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