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Shrubland longevity and rare plant species in the northeastern United States

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Abstract

Thickets in the northeastern United States typically consist of opportunistic, early successional plants, a category that includes few if any rare species. Nonetheless, some of the region's globally rare plants and many regionally rare, disjunct and edge-of-range species are shrubs or herbaceous plants with high fidelity to shrublands. Some shrub-dominated ecosystems harbor clusters of rare plant taxa. Shrubland longevity seems to be the key. Because shrublands tend to be isolated and small in the Northeast and dispersal of rare plants is further limited by the sparseness of propagule-exporting populations, multiple rare species are likely to accumulate and persist only in shrublands that are stable over long time periods. Zones at the two extremes of the soil moisture gradient, at the highest elevations, and exposed to marine salt spray often are occupied by relatively stable shrublands that include rare plant populations. In a few cases, shrublands also have persisted on mesic, fertile soils for long enough to accumulate clusters of rare plant species. High rates of human disturbance might provide an explanation, but it is unlikely that such disturbance regimes would have been sustained uninterrupted over centuries and across the transition from Native American to European land-use practices. Alternatively, mesic shrublands could persist with only moderate rates of disturbance and through extended disturbance-free periods if the plants themselves are slowing succession or changing its trajectory. Evidence is reviewed that some shrubs may alter the environment and ecosystem processes in ways that favor their own ability to persist and reproduce while making a site less hospitable to the establishment of forest trees. Plants ordinarily thought of as early successional species do the opposite, changing the environment in ways that ultimately hinder their own ability to persist by incidentally making the site more hospitable to species that outcompete them. Hypothesized processes that sustain northeastern shrublands on mesic soils involve fire, frost pockets, soil hardpans, soil acidification, nitrogen sequestration, and allelopathy. They can account for shrubland persistence if dominant shrub species (in some cases with a boost from human activity) foster one or more of these processes to the greater detriment of their potential competitors than to themselves. Subordinate shrubland species, including rare plants, do not need to be active in fostering such processes to benefit from them.

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1. Introduction

In the northeastern United States, shrublands are not generally considered as hotspots for rare spe-

cies or for plant species richness. The most common shrublands in the region, including blackberry and raspberry (*Rubus* spp.) briar patches, overgrown forest clearcuts, and scrub oak (*Quercus ilicifolia*) thickets are not often destinations for botanical field trips. But there are a few noteworthy exceptions.

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Rare plants and animals tend to occur in clusters; several such clusters in the Northeast encompass shrublands. Among the richest examples are alpine communities in the White Mountains of New Hampshire (62 rare plant taxa, including 8 that are globally rare and 15 shrubs; W. Nichols, personal communication). Many of the shrubland types themselves rank as globally rare and endangered, for example, hudsonia river beach in Maine (Gawler, 2001) and bog birch-poison-sumac-shrubby-cinquefoil shrubland in New Jersey (Breden et al., 2001). Typically the globally rare shrublands are among those harboring clusters of rare plants and animals. Globally imperiled sandplain heathlands in coastal Massachusetts, for example, are home to six rare herbaceous plants (including one that is globally rare), four rare shrubs (one globally rare), and eight rare animals (Swain and Kearsley, 2001).

Why do some shrublands harbor clusters of rare species when most shrub-dominated landscapes in east-central North America are full of weedy, opportunistic, and invasive species? One hypothesis is that only a few of the region's shrublands, isolated as they are in a sea of forest, have persisted long enough for multiple rare species to accumulate. Populations of rare plants by definition are sparse or highly localized, limiting the availability and dispersal of propagules. The majority of shrublands, as early successional communities, are too short-lived to be a likely "target" for rare species' seeds or spores or to allow the establishment of self-sustaining populations.

Because thickets tend to be ephemeral in a year-round moist climate, the idea of shrublands persisting for centuries or millenia in such a climate seems paradoxical. Conditions in the northeastern United States are usually highly favorable for rapid colonization of disturbed sites by trees: warm summers, high year-round precipitation, and abundant organic residues in soils of all but the most severely disturbed sites, providing a ready supply of nutrients. Wherever shrublands persist for more than a decade or so, something is slowing or preventing the usual colonization by trees.

Judging from the worldwide distribution of shrubs, the shrubby growth form predisposes a plant to be more stress-tolerant than the tree form. Shrubs live virtually everywhere trees are found, but they also occupy vast areas where trees are sparse or absent. Instances include temperate areas with dry summers and winter monsoons (e.g., chaparral, matorral, garrigue, maqui,

fynbos, mallee), boreal and alpine zones beyond the latitudinal or altitudinal limits of tree growth (tundra), the moister deserts (desert scrub), and wet heathlands. In east-central North America, environments where shrub-dominated communities persist the longest are near the two extremes of the soil moisture gradient, near the highest elevations, and in places exposed to marine salt spray. These environments are resistant in varying degrees to tree invasion. Trees that do manage to get a foothold often are either short-lived, as in the wettest shrub swamps, or exhibit a dwarfed, shrub-like growth form, as in alpine krummholz.

An alternative way for shrublands to be long-lived in the northeastern United States involves high rates of disturbance. However, disturbances would have to occur without interruption for centuries and more frequently than the recovery time of forests under the influence of the local soil and climate. They would have to fall consistently within a window of severity to which trees are sensitive and shrubs are tolerant. If anthropogenic, they would also have to have been sustained across the transition from American Indian land-use practices to Europeans' very different ways of managing the land, and on through the present day.

As unlikely as such a combination of circumstances seems to be, a few shrublands in the Northeast are believed to have persisted for centuries (perhaps even before European settlement) despite living where climate and soils favor rapid displacement by forests. These stable shrublands fall into at least two categories, both rich in rare plants. One consists of mesic barrens on flat-topped plateaus at 600–1400 m elevation, which are surrounded, atop the same surficial geology and terrain, by hardwood forests. Two mesic shrubland sites are well known. One (less than 1 km² in extent) is in the Panther Knob and Kile Plateau sections of North Fork Mountain, West Virginia (Harmon, 1981); the other (approximately 22 km²) is on the southern Pocono Plateau, Pennsylvania (Latham et al., 1996). The second category is the dwarf pine barrens or pine plains, which consist of dwarfed, multi-stemmed pitch pine (*Pinus rigida*) and oaks (*Quercus* spp.) living as shrubs together with true shrubs. Occurring on sandy soils in southern New Jersey (53 km²) and on Long Island, New York (4 km²), the pine plains are surrounded, again on the same surficial geology and terrain, by full-stature pine–oak forests (Lutz, 1934; Olsvig et al., 1979;

Gibson et al., 1999). A shrubland that seems to fall into both categories occurs at Sams Point in the Shawangunk Mountains in New York, where an area of dwarf pitch pines and other shrubs (0.2 km^2) occupies mesic soils on a flat-topped plateau (McIntosh, 1959; Laing, 1994).

Testing the hypothesis (and its underlying assumptions) that rare species clusters indicate shrublands of extraordinary longevity in a mostly forested region requires: (1) evidence of shrubland persistence for several centuries or longer and (2) testable explanations of the means by which succession may be slowed, interrupted or redirected over such long time spans. In this paper, I describes patterns in rare plant species occurrence in shrublands across the northeastern United States, from Maine to Maryland and West Virginia. Because short-lived, early successional thickets and shrublands of intermediate longevity, such as certain scrub oak barrens, harbor few or no rare plants, this paper focuses mainly on shrublands that have existed in their current location since before Europeans colonized east-central North America. Both short- and long-lived shrublands are crucial habitats for many animal species (see Dettmers, 2003; Fuller and DeStefano, 2003; Wagner et al., 2003); the short-lived shrubland types are treated at length elsewhere in this volume (e.g., Foster and Motzkin, 2003; Lorimer and White, 2003; Somers, 2003). This paper concludes with a discussion of the hypothesis that an exceptional few of the very old shrublands may persist, in part, by plants acting as “ecosystem engineers”, actively changing local conditions.

2. Patterns of rare plant distribution in northeastern shrublands

Of the 165 vascular plant taxa in the 12 northeastern states classified as globally rare (i.e., ranked G3 or G5T3 and higher; see Table 1 for the definitions of ranks), 17 (10%) are shrubs, including one liana. At least 20 (12%), including 7 of the shrubs, typically inhabit shrub-dominated communities. Altogether, globally rare shrubs together with globally rare vascular plants typically living in shrublands comprise 30 taxa in the Northeast (Table 1), 19% of all globally rare vascular plants in the region.

Recent statewide community classifications in six northeastern states show a range of 7–23 shrub-dominated community types (mean $17.5 \pm 2.8 \text{ S.E.}$) in each state, representing 9–22% of each state's vascular plant-dominated communities.¹ In the three published statewide classifications that assign global rarity ranks to the communities themselves, 20% (state of Maine), 28% (state of New York), and 42% (state of New Jersey) of the shrubland communities of these states are considered to be globally rare and imperiled.

Except where stated otherwise, “rare” in this paper refers to globally rare and regionally rare plant or animal taxa, that is, species and subspecies ranked as critically imperiled (S1), imperiled (S2), or very rare or highly restricted in range and thus vulnerable (S3) in the state where the shrubland under discussion is located. Three patterns can be discerned from the limited data that pertain to distributions of rare plants in shrublands of the Northeast.

1. The communities and sites with the largest numbers of rare plants, 30 to over 100 taxa, are those in which shrubby areas comprise only a part, and the shrub-dominated sections contain few or none of the rare plants. Examples include serpentine barrens, coastal plain ponds, calcareous fens, coastal plain and glacial outwash pine barrens, and Great Lakes beach-dune-sandplain complexes.
2. The shrublands that are richest in rare vascular plants have on the order of 6–15 rare plant taxa. They fall into five main categories:
 - (a) Sandplains near the seacoast, e.g., on Cape Cod, Nantucket Island, Martha's Vineyard (Massachusetts), Block Island (Rhode Island), and Long Island (New York).
 - (b) Atlantic coastal dune thickets, e.g., on capes and barrier islands in New Jersey, Delaware, and Maryland.
 - (c) Alpine/subalpine dwarf shrub and krummholz communities, at nearly 50 sites, mainly in the White Mountains, New Hampshire, but also near the highest summits in Maine, Vermont, and New York (Sperduto, 1997).

¹ Massachusetts, 11 (10%; Swain and Kearsley, 2001); Maine, 23 (22%; Gawler, 2001); New Jersey 21 (15%; Breden et al., 2001); New York, 21 (15%; Edinger et al., 2002); Pennsylvania, 22 (21%; Fike, 1999); Vermont, 7 (9%, Thompson and Sorenson, 2000).

Table 1

Globally rare vascular plants inhabiting shrublands and globally rare shrubs (boldface) in the 12 northeastern states, derived from the list of all 165 vascular plant taxa in the region currently ranked G3 or G5T3 and higher

Rare taxon	Common name	Rank ^a	States ^b	Habitat categories ^c
<i>Alnus maritima</i>	Seaside alder	G3	DE, MD	Lake/pond margin, streambank
<i>Amelanchier nantucketensis</i>	Nantucket shadbush	G3Q	MA, MD, ME, NY	Grassland, upland shrubland/thicket
<i>Berberis canadensis</i>	American barberry	G3	MD, PA, WV	Upland forest/woodland
<i>Cacalia suaveolens</i>	Sweet-scented Indian-plantain	G3	CT, MD, NJ, NY, RI	Upland forest/woodland, streambank, upland shrubland/thicket
<i>Carex polymorpha</i>	Variable sedge	G3	CT, DE, MA, MD, ME, NJ, NH, NY, PA, RI, WV	Upland forest/woodland, upland shrubland/thicket
<i>Carex wiegandii</i>	Wiegand's sedge	G3	MA, ME, NH, NY, PA, VT	Bog, marsh, swamp shrubland/thicket
<i>Crataegus pensylvanica</i>	Pennsylvania hawthorn	G3Q	NJ, PA	Upland forest/woodland, ruderal, upland shrubland/thicket
<i>Delphinium exaltatum</i>	Tall larkspur	G3	MD, PA, WV	Upland forest/woodland, open rock outcrop, upland shrubland/thicket
<i>Dioscorea villosa</i> var. <i>hirticaulis</i>	Hairy-stemmed wild yam	G4G5T3Q	MD, NJ	Upland forest/woodland, ruderal, upland shrubland/thicket
<i>Euphorbia purpurea</i>	Glade spurge	G3	DE, MD, NJ, PA, WV	Swamp forest/woodland, swamp shrubland/thicket
<i>Gaylussacia brachycera</i>	Box huckleberry	G2G3	DE, MD, PA, WV	Upland forest/woodland
<i>Gnaphalium helleri</i> var. <i>micradenium</i>	Small everlasting	G4G5T3?	NJ	Upland forest/woodland, upland shrubland/thicket
<i>Ilex collina</i>	Long-stalked holly	G3	WV	Bog, streambank, swamp forest/woodland
<i>Liatris borealis</i>	Northern blazing-star	G3	NH, NY	Upland forest/woodland, grassland, upland shrubland/thicket
<i>Listera auriculata</i>	Auricled twayblade	G3	ME, NH, NY, VT	Swamp forest/woodland, swamp shrubland/thicket
<i>Litsea aestivalis</i>	Pondspice	G3	DE, MD	Lake/pond margin, swamp forest/woodland
<i>Monarda fistulosa</i> var. <i>brevis</i>	Smoke Hole bergamot	G5T1	WV	Upland forest/woodland, grassland, upland shrubland/thicket
<i>Paxistima canbyi</i>	Canby's mountain-lover	G2	PA, MD, WV	Open rock outcrop
<i>Pycnanthemum clinopodioides</i>	Basil mountain-mint	G2	CT, DE, MA, MD, NJ, NY, PA, WV	Upland forest/woodland, lake/pond margin, upland shrubland/thicket
<i>Pycnanthemum torrei</i>	Torrey's mountain-mint	G2	CT, DE, MD, NH, NJ, NY, PA, WV	Upland forest/woodland, upland shrubland/thicket
<i>Rosa blanda</i> var. <i>glabra</i>	Northern rose	G5T3Q	ME	Upland forest/woodland, grassland, seashore/lakeshore
<i>Rubus gnarus</i>	Pollocks Mill blackberry	G3?	NJ	Upland shrubland/thicket
<i>Rubus hypolasius</i>	Pineland dewberry	G1?Q	NJ	Swamp forest/woodland, swamp shrubland/thicket
<i>Rubus novocaeasarius</i>	New Jersey dewberry	G1?	NJ	Bog, swamp shrubland/thicket
<i>Rubus originalis</i>	Cold Spring blackberry	G3?	NJ	Upland forest/woodland, upland shrubland/thicket
<i>Rubus osryifolius</i>	Highbush blackberry	G3?Q	NJ	Upland shrubland/thicket
<i>Spiraea septentrionalis</i>	Northern meadow-sweet	G3?	ME	Alpine
<i>Spiraea virginiana</i>	Virginia spiraea	G2	PA, WV	Open rock outcrop, streambank
<i>Viola brittoniana</i> var. <i>pectinata</i>	Cut-leaf coast violet	G4G5T3?Q	NJ	Bog, swamp shrubland/thicket
<i>Vitis rupestris</i>	Sand grape	G3	MD, PA, WV	Open rock outcrop, streambank

^a Global ranks: G1, critically imperiled; G2, imperiled; G3, very rare or highly restricted in range and thus vulnerable; G4, apparently secure; G5, demonstrably secure; T1, T2, T3, rank of subspecies or variety; double ranks and ranks followed by ?, global status uncertain; Q, taxon of questionable or uncertain taxonomic standing, i.e., one that taxonomists disagree whether to regard as a full species, subspecies, variety, or trivial form.

^b Sources: Connecticut Environmental and Geographic Information Center (2002), Enser (2000; for Rhode Island), Maine Natural Resources Information and Mapping Center (1999), Maryland Wildlife and Heritage Division (2001), Massachusetts Natural Heritage and Endangered Species Program (2001), McAvoy (2001; for Delaware), New Jersey Office of Natural Lands Management (2001), New Hampshire Natural Heritage Inventory (2002), Pennsylvania Natural Diversity Inventory (2001), Vermont Nongame and Natural Heritage Program (2000), West Virginia Natural Heritage Program (2000), Young (2001; for New York).

^c Main sources: Fernald (1950), Gleason and Cronquist (1991), Radford et al. (1968), Rhoads and Block (2000), Strausbaugh and Core (1970), Swain and Kearsley (2001). Additional sources for particular species: Aiken et al. (2001), R. Bartgis (personal communication), Bruce et al. (1991), D.S. Cameron (personal communication), C.T. Frye (personal communication), W.A. McAvoy (personal communication), W. Nichols (personal communication), Paris (1991), R. Popp (personal communication), D.B. Snyder (personal communication).

- (d) Heath-dominated peatlands, widespread in northeastern North America.
- (e) “Mesic barrens” (persistent shrublands on moist, fertile, loamy soils) on flat-topped plateaus of intermediate elevation, at one site each in New York (McIntosh, 1959), Pennsylvania (Latham et al., 1996), and West Virginia (Harmon, 1981).
- 3. Many shrublands harbor numerous rare animal species but few or no rare plants. This category includes the majority of shrublands with abundant scrub oak (*Q. ilicifolia*) but not all of them. Some, hypothesized to be the oldest among the shrublands in this category, are also rich in rare plant species.

For example, of the three largest shrubland complexes in Pennsylvania, all with large areas dominated by scrub oak, a substantial portion of only one is known to pre-date European settlement. The 19th century origin of Scotia Barrens (36 km^2) is recorded in detail (Westerfield, 1939). The history of the Moosic Mountain barrens (24 km^2) is poorly known but the dearth of historical description suggests a relatively recent origin. In contrast, expansive shrublands near the center of the southern Pocono Plateau barrens (where currently the shrub-dominated area totals 40 km^2) were well documented by early explorers before Europeans settled locally (Latham et al., 1996). Scotia Barrens are known to have 3 rare plants and 14 rare animals (Stack et al., 1991) and the Moosic Mountain barrens have no known rare plants and 2 rare animals (Cameron et al., 1997). The Pocono barrens, on the other hand, have at least 16 rare plants and 22 rare animals² (Pennsylvania Natural Diversity Inventory, unpublished data).

A thorough inventory is needed to determine whether a similar pattern of correspondence between shrubland age and the number of rare plant species present is repeated throughout the northeastern United States. The greatest challenge will be to estimate how

long each major shrubland site has been in shrub cover. This is possible only where there are pertinent historical records and a well-preserved stratigraphic record of pollen and charcoal. Unfortunately, these types of evidence are lacking for many sites and where they do exist, finding them can be difficult and analyzing them is painstaking and expensive. Other examples of sites in the region containing shrublands that may pre-date European settlement include the Long Island pine barrens, New York, with 54 rare plants and 19 rare animals (G.J. Edinger and M. Jordan, personal communication), the Shawangunk Mountain barrens, New York, with 16 rare plants and 9 rare animals (J.E. Thompson, personal communication), the State Line serpentine barrens, Pennsylvania and Maryland, with 40 rare plants and 45 rare animals (Pennsylvania Natural Diversity Inventory, unpublished data), Panther Knob, West Virginia, with 10 rare plants and 5 rare animals (P.J. Harmon, personal communication), and Assateague Island, Maryland and Virginia, with 21 rare plants and 24 rare animals (C. Lea, personal communication).

3. Historical and palynological evidence for shrubland antiquity

Historical evidence for the great longevity of shrublands in east-central North America is scant. Some of the most thorough chronologies are for shrublands in New England (e.g., Motzkin et al., 1999a,b; Foster et al., 2002; Eberhardt et al., 2003), with historical accounts dating back to the early 1600s and, in some cases, palynological data reaching back thousands of years. However, the evidence has confirmed post-European-settlement origins for most of these shrublands.

One of the best documented pre-European-settlement shrublands is on the southern Pocono Plateau in northeastern Pennsylvania (Latham et al., 1996). The historical record is exceptionally complete partly because European occupation of the site was relatively late, some 200 years after the founding of the earliest European settlements in the Northeast. The first known written mention of the area's vegetation consists of annotations on a 1737 sketch map by the Pennsylvania colony's surveyor general describing “... a mountainous barren country abounding with pines ...” (Davis, 1876). Isaac Zane, commissioned by

²Counts of rare animal species are, without doubt, underestimates. Animal surveys are much more laborious than for vascular plants, are rarely exhaustive, and often are limited to vertebrates and Lepidoptera. As a rule, most of the animal species likely to be present at any given site remain unexamined, including most spiders, mites, centipedes, springtails, thrips, beetles, wasps, ants, flies, aphids, nematodes, earthworms, and members of many other, smaller groups.

the colonial government to help build a town for a group of Lenape Indians displaced by European settlers, in 1758 traversed the southern Pocono Plateau, where he recorded seeing “a poor Sovana which the Indians burn once in 3 or 4 years and kills such scrub wood as grow on it” (Coates, 1906). Such a record, noting a detail of Native American burning practices in eastern North America, is rare indeed. Passing through in 1779, various members of a United States military expedition against the Iroquois wrote of “sunken swamps and burning plains”, “the ground universally covered with brush by the name of ground oak”, “the most barren part of the country I ever saw”, a “great Swamp, which is interspersed & barren piney Spots throughout very Stony”, and land “very poor & barren & I think Such as will never be Inhabited” (Cook, 1887).

The first botanist to visit the area was Frederick Pursh, in 1807, when the southern Pocono Plateau was virtually uninhabited and still untouched by lumbering. He noted, on “coming to the barrens in the top [of the plateau], I soon found . . . *Rhodora* [*Rhododendron*] *canadensis* grows here in great plenty”

(Beauchamp, 1923). In 1832, soon after settlers of European origin began making their homes in the area, naturalist and traveler Maximilian, prince of the German kingdom of Wied, passed through, observing, “. . . we were surrounded, as far as the eye could reach, with woods or thickets of low oaks, from which numbers of slender, half-dried, short-branched pines (*P. rigida*) shot up. . . . in the dry season these woods have often been destroyed by extensive conflagrations . . .” (Thwaites, 1906). Evidently by then the new residents had taken up the American Indian practice of burning, or they at least were sources of accidental ignition. Botanist Thomas C. Porter described, on a visit in 1859, “woods, which are here very open . . . Fire . . . has no doubt done its part. These . . . barrens, are very extensive & their vegetation quite uniform” (Porter, 1859). The 77 species mentioned by Porter include virtually all that characterize the shrublands today (see Fig. 1).

The shrublands of the southern Pocono Plateau may have gone the way of many others in the northeastern United States and succeeded to forest if it were not for



Fig. 1. Pocono mesic till barrens, northeastern Pennsylvania. Dominant shrubs are sheep-laurel (*K. angustifolia*), common lowbush blueberry (*V. angustifolium*), rhodora (*R. canadense*), and scrub oak (*Q. ilicifolia*). Other abundant woody species include black chokeberry (*Aronia melanocarpa*), gray birch (*B. populifolia*), teaberry (*Gaultheria procumbens*), black huckleberry (*Gaylussacia baccata*), pitch pine (*P. rigida*), swamp dewberry (*Rubus hispida*), other lowbush blueberries (*V. myrtilloides*, *V. pallidum*), and witherod (*Viburnum cassinoides*).

a particular land-management custom of the earliest European residents. Beginning in the 19th century, humans that harvested blueberries and huckleberries enhanced production by frequently setting fires (Anonymous, 1898; Rowland, 1957). Single fires of 10–20 km² were not uncommon from around 1900, when records were first kept, until the first establishment of effective fire suppression in the early 1960s (Pennsylvania Bureau of Forestry, unpublished data).

Historical evidence pertaining to pre-settlement shrublands in the Northeast is rare; many more eyewitness accounts have been uncovered pertaining to agricultural fields, abandoned old fields, and grasslands (Whitney, 1994; Askins, 1997; Lorimer, 2001). There are a few accounts of pre-settlement scrub oak stands that no longer exist, for example, in the vicinity of New Haven, Connecticut (Dwight, 1823, cited by Motzkin et al., 1999b). Some present-day shrublands date back to early European settlement but no further. Forest clearing or subsequent catastrophic wildfires eliminated the forest and fires or other disturbances since then have prevented its reestablishment for most of recorded history. Well known examples include the shrublands of Waterboro Barrens, Maine (Copenheaver et al., 2000), Montague Plain, Massachusetts (Motzkin et al., 1999a,b), Scotia Barrens near State College, Pennsylvania (Westerfield, 1939; Clarke, 1946), and Dolly Sods, West Virginia (Allard and Leonard, 1952). These sites have clusters of rare animal species, mainly specialist-feeding insects associated with shrub oaks and other common shrubland species (Wagner et al., 2003), but few rare plants. Thus, even in shrublands 150–300 years old, plant species diversity may be relatively low and rare plant species are few or absent.

The systematic unearthing and comparison of site histories are key steps in testing the hypothesis linking shrubland longevity to the incidence of rare plant species clusters. One approach would be to compare sites found to have supported shrubland continuously since before European occupation with shrubland sites of similar bedrock, soils, topography, climate and hydrology that are known to have been forested at the time of European contact. For example, shrubby plateaus on North Fork Mountain, West Virginia are among the richest sites in the state for rare plants, with 20 taxa including 4 that are globally rare. Dolly Sods is a larger shrubland complex on the plateau along the

Allegheny Front; its climate, surficial geology, and dominant species composition are similar to those of North Fork Mountain, the next ridge to the east, but few rare plants have been found there. It is well documented that Dolly Sods was covered by a dense red spruce (*Picea rubens*) forest at the time of first European contact (Allard and Leonard, 1952), which never recovered after clearcutting in the early to mid-19th century. So far the evidence for the age of the North Fork Mountain shrublands is scant, but they may date far back into prehistoric times (Core, 1949).

There are few published analyses by paleobiologists of pollen cores from shrublands in the northeastern United States except for peat bogs, which tend to be small and surrounded by forest. An unpublished 9000-year chronology from a swamp next to the Shawangunk Mountain dwarf pine barrens (Laing, 1994) showed an abrupt increase in percentages of pollen from pitch pine and Ericaceae at 1920 ± 50 years ago, followed by sustained high levels to the present. There is stratigraphic evidence for similar changes in vegetation well before European contact at several other locations across the northeastern United States (e.g., Patterson and Backman, 1988; Patterson and Sassaman, 1988; Clark and Royall, 1996) and elsewhere in eastern North America (e.g., Davis, 1985; Delcourt and Delcourt, 1997, 1998). I will return to this line of evidence later in discussing the link between the region's shrublands and fire.

4. Do long-lived mesic shrublands represent an alternative successional pathway?

Most persistent shrublands in the northeastern United States are in extreme environments: perennially wet peatlands, dry sands, cold mountain peaks, or shores exposed to salt spray. At a few sites, however, long-lived shrublands occupy sites as hospitable as those of nearby forests (e.g., Ehrenfeld et al., 1995; Latham et al., 1996). There is nothing obvious about topography, soil moisture, or other abiotic factors to explain the sharp boundaries between them and surrounding full-stature forests. Furthermore, the plant species composition of these shrublands is conspicuously different from early successional thickets in nearby forest openings or old fields with the same soil type and topographic position, which establishes

that they are not just examples of arrested succession. Some ecologists have approached similar conundrums in other ecosystems with the hypothesis that, in certain cases, different sets of dominant species can force alternative successional pathways with different end points (e.g., Laycock, 1991; Knowlton, 1992; Wilson and Agnew, 1992).

The most difficult problem encountered by researchers in determining whether two communities occupying the same environment represent alternative successional trajectories with different end states is demonstrating that they occupy the “same environment”. This condition is difficult to prove, partly because feedback loops driven by some species alter the environment (Peterson, 1984; Petraitis and Latham, 1999) and partly because showing no difference poses the difficult statistical problem of accepting a null hypothesis with a high level of confidence (e.g., see Cohen, 1988). Also, if a species assemblage is relatively stable, its replacement by another persistent state requires a perturbation event severe enough to bring about drastic change in the densities of resident organisms (Bender et al., 1984), thus temporarily changing environmental conditions. The ideal experiment would be to subject replicate sites occupied by one of two postulated alternative community states to catastrophic disturbance, and see whether some fraction of the replicates succeed to the other state. This is practical in some ecosystems (e.g., Petraitis and Dudgeon, 1999). However, in forests and shrublands, mimicking the natural disturbances that kill most of the dominant plants in a replicated experiment would be monumentally expensive, in some cases unethical, and measurable responses of key variables might take decades to occur.

Despite these problems, “natural experiments” or observational studies along multiple independent lines of investigation are a means to begin amassing evidence for or against the hypothesis that two adjacent, dissimilar communities occupy the same environment. For example, since the late 19th century explanations for the stunted nature of the pine plains vegetation in the New Jersey Pine Barrens focused on localized differences in resource availability and stressful conditions (e.g., nutrient-poor soils, aluminum toxicity, a hardpan, and sandier soil texture). Research over the years has falsified these hypotheses one by one (Gibson et al., 1999). Soil studies have shown that differences between the pine plains and the surrounding pine–oak forests are

minimal or lacking (Lutz, 1934; Andresen, 1959). Phytometer experiments using eastern white pine (*Pinus strobus*) showed that the species is equally productive in both environments (Little, 1972). The New Jersey pine plains have been found to have higher rates of mean net annual aboveground biomass production than the surrounding full-stature forests (Buchholz and Good, 1982). Genetic studies (reviewed by Gibson et al., 1999) have shown that the dwarf pitch pines in the pine plains are a genetically distinct ecotype, whose distinguishing traits include early sexual reproduction, serotinous cones, multi-stemmed growth form, and prolonged stump-sprouting after top-kill by fire. A consensus has begun to emerge over the last 25 years that the environment is not different between the pine plains and surrounding pine–oak forests and the striking differences are produced mainly by the dominant plants (Good et al., 1979; Gibson et al., 1999).

Studies of soil and biomass nutrient capital and soil moisture variation in the mesic till barrens of the southern Pocono Plateau in Pennsylvania have yielded strong evidence that mineral soils and soil parent material do not explain the distribution of shrublands there (Eberhardt and Latham, 2000; Wibarske, 2002). The sharp boundary between shrubland and forest corresponds to no detectable discontinuity or gradient in soil characteristics except in the organic layer, which is developed mainly by the plants themselves together with microbes, animals, and fire. Furthermore, the disparities contradict common wisdom about northeastern shrublands: where significantly different, shrubland soils have slightly higher concentrations and amounts of nutrients than forest soils (Wibarske, 2002). Factorial design and high replication enabled the detection of very small differences. Whether the nutrient differences that run counter to prediction are large enough to affect vegetation patterns is unknown.

Large differences in C:N ratios were found even though total soil nitrogen does not differ between shrubland and forest. In biomass, litter, and soil organic matter, C:N ratios were higher in shrubland than in forest and the Oa horizon was larger in shrubland (Wibarske, 2002), indicating an accumulation of recalcitrant, nitrogen-sequestering decomposition residues in this horizon. In another study, *Carex pensylvanica*, a sedge that lives in both Pocono mesic till barrens and neighboring forests, was used as the phytometer in a greenhouse bioassay comparing nitrogen availability in

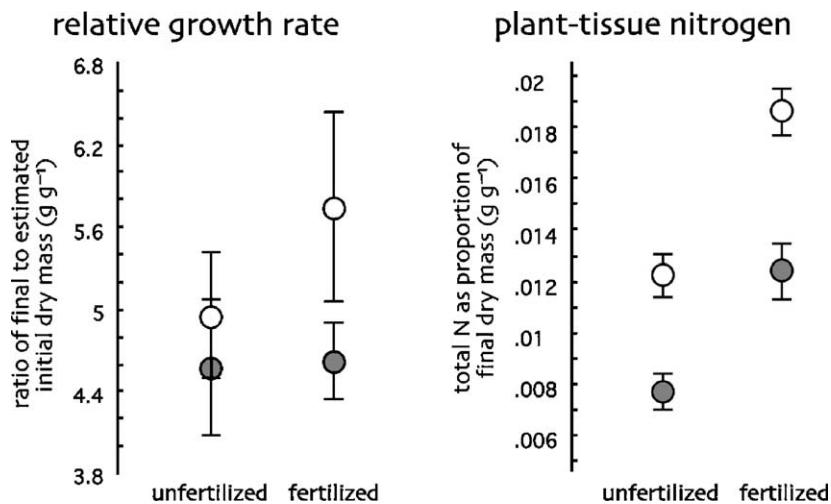


Fig. 2. Results of a greenhouse experiment in which Pennsylvania sedge (*C. pensylvanica*) was grown in soil collected in the Pocono mesic till barrens (filled circles) and adjacent forests with the same soil parent material and topographic position (open circles). Error bars are 95% confidence limits.

soils from shrubland and adjacent forest (Yorgey and Latham, 1999). Half of the replicates in each soil type were fertilized with ammonium nitrate. After 4 weeks, nitrogen concentration in plant tissue was nearly 1.6 times as high in plants grown in forest soil as in shrubland soil (Fig. 2). Plants responded to fertilization by increasing biomass growth rate in forest soil but not in shrubland soil, but they increased nitrogen acquisition at the same rate in both soils (Fig. 2). These results suggest that the differences between shrubland and forest in this system are biotic in origin.

The most striking differences between the Pocono mesic till barrens and surrounding vegetation are tree species distributions, including age structure. Almost all of the tree and tall shrub species that are common to abundant in the surrounding forest, including early-serial stages after logging and old-field abandonment, are absent or nearly absent in the mesic shrubland. This group includes American beech (*Fagus grandifolia*), mountain holly (*Ilex montana*), mountain-laurel (*Kalmia latifolia*), tamarack (*Larix laricina*), blackgum (*Nyssa sylvatica*), pin cherry (*Prunus pensylvanica*), black cherry (*P. serotina*), white oak (*Quercus alba*), scarlet oak (*Q. coccinea*), black oak (*Q. velutina*), great-laurel (*Rhododendron maximum*), mountain azalea (*R. prinophyllum*), swamp azalea (*R. viscosum*), and eastern hemlock (*Tsuga canadensis*). At the seedling stage, nine of these are fairly common

on the forest floor and in forest openings but none are present in the shrubland. Many other trees that are less abundant in local forests are wholly absent in the shrublands as adults or seedlings, including sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), sweet birch (*B. lenta*), American chestnut (*Castanea dentata*), white ash (*Fraxinus americana*), tuliptree (*Liriodendron tulipifera*), chestnut oak (*Quercus montana*), and northern red oak (*Q. rubra*). A few trees and tall shrubs that are common in the forest occur sparsely in the shrubland as seedlings and saplings but are essentially absent as large individuals, including red spruce (*P. rubens*), quaking aspen (*Populus tremuloides*), sassafras (*Sassafras albidum*), and highbush blueberry (*Vaccinium corymbosum*). A few species of small trees extend across both habitats, including downy shadblush (*Amelanchier arborea*), smooth shadblush (*A. laevis*), and gray birch (*Betula populifolia*), but only one abundant tree of the forest canopy—red maple (*Acer rubrum*)—also occurs as seedlings, saplings and adults in the shrubland.

5. How positive feedbacks may foster shrubland persistence?

How can it be that some shrublands on moist, fertile soils in east-central North America apparently are

stable over very long time spans? Here I present the hypothesis that succession was slowed, interrupted or redirected over long periods due to a fortuitous interaction of disturbance, due at least in part to human activity, and unusual traits of certain dominant shrub species. Those traits resulted in the plants themselves changing the environment and ecosystem processes in ways that incidentally led to changes in successional patterns.

When two very different species assemblages are found side-by-side on the landscape, such as a forest and a shrubland, and both persist for a long time, the habitat heterogeneity is traditionally assumed to arise from some underlying physical gradient or discontinuity. This is often a change in bedrock type, soil hydrology or solar aspect. In contrast, recent work on some shrublands dominated by ericaceous species has attributed their persistence to a set of positive (i.e., self-reinforcing) feedbacks arising from the dominant ericaceous shrubs (Mallik, 1993, 1995, 2001; Inderjit and Mallik, 1996a,b, 1999; Bradley et al., 1997a,b, 2000). The environmental changes “engineered” by the dominant shrubs are especially likely to forestall forest succession where it is also delayed by cool, cloudy climates that slow plant growth and microbial decomposition (Mallik, 1995). The climates of the Pocono Plateau in Pennsylvania and North Fork Mountain in West Virginia resemble those of other places where research has shown strong resistance by mesic heathlands to forest invasion, for example, northern Europe (Gimingham, 1972; Read, 1984; Souto et al., 2000), Newfoundland (Damman, 1971, 1975; Mallik, 1995), British Columbia (de Montigny and Weetman, 1990), and higher elevations in the southern Appalachians (Dighton and Coleman, 1992; Nilsen et al., 1999).

Each positive feedback has two components: an environmental change brought about by plants and tolerance of the change by those same plants. The dominant plants of mesic heathlands acidify the soil, and they are highly tolerant of soil acidity (Read, 1984). They produce recalcitrant litter, which slows nitrogen and phosphorus mineralization by soil microbes (Grubb et al., 1969; Damman, 1971; Northup et al., 1995, 1998), but they also join with ericoid mycorrhizal fungi, which decompose and take up organically bound nitrogen and phosphorus before they can be mineralized by soil microbes and made

available to plants with other types of mycorrhizal relationships (Read, 1983; Dighton and Coleman, 1992; Leake, 1992). Some shrubland plants are allelopathic, tolerant of their own toxicity and any induced effects on soil microbial communities and nutrient cycling (Read, 1984; Mallik, 1995; Inderjit and Weiner, 2001). The resulting positive feedbacks can lead to species assemblages that often superficially resemble early successional stages but persist for a long time by resisting invasion (Laycock, 1991; Wilson and Agnew, 1992; Northup et al., 1998). True early successional plants are intolerant of the environmental changes they and other plants produce, especially shade.

Members of the Ericaceae exemplify the coupling of low-nutrient-tolerance with the active reduction of nutrient availability. The family includes some of the strongest soil acidifiers among vascular plants (Read, 1984; Griffiths et al., 1992; Marschner, 1992) and, not surprisingly, they are also among the most tolerant of high soil acidity. The high tannin and lignin and low nitrogen content of sclerophyllous shrubs makes their leaf litter and other organic debris resistant to decomposition, tying up nutrients and slowing down their recycling (Melillo et al., 1982; Kuiters, 1990; de Montigny and Weetman, 1990). The aptly termed “afterlife effect” (Wardle et al., 1998) of recalcitrant litter falls hardest on the growth of plants that are sensitive to low nutrient availability, including the seedlings of many forest tree species. Plants that are tolerant of low nutrients, including sclerophyllous shrubs, are less affected (Chapin, 1980; Read, 1984; de Montigny and Weetman, 1990). The ways an ericaceous plant can tolerate low nitrogen availability include inherently slow growth, high nitrogen-use efficiency, and the ability of its ericoid fungal partner to transport amino acids and other complex nitrogen sources to its host before they are mineralized to forms available to many other plants (Read, 1983; Leake, 1992).

Recent research by Robin Bloom and Azim Mallik in long-lived mesic shrublands in Newfoundland has shown that the shrubland-sustaining feedbacks may be more pervasive than previously thought, varying not only between shrubland and adjacent forest in concert with the dominant species composition, but also varying between habitats within a species. Sheep-laurel (*Kalmia angustifolia*) is one of the dominant species in the Pocono mesic till barrens as well as in persistent

heathlands covering vast areas of Newfoundland where closed-canopy forests of black spruce (*Picea mariana*) stood before widespread clearcutting in the mid-20th century. Sheep-laurel is known to be a strong inhibitor of tree regeneration where growing in dense stands unshaded by a tree canopy (Mallik, 1993, 1995, 2001; Inderjit and Mallik, 1996b, 1999; Bradley et al., 1997a,b, 2000). However, its tissue and litter chemistry is sharply different where growing in the shade of a forest, where its effect on soil factors associated with tree seedling establishment is relatively benign (R. Bloom and A.U. Mallik, unpublished data).

Another process that helps to stabilize some heathlands is the presence of an iron or manganese-cemented hardpan, whose formation may be fostered by ericaceous vegetation (Damman, 1965; McKeague et al., 1968; Gimingham, 1972) or other soil-acidifying plants (Ugolini and Mann, 1979). Hardpans are formed when sesquioxides (hydrous oxides of iron and other metals) and stable organic molecules leach from the litter and humus, travel downward in the soil solution, and precipitate out in a narrow band at a particular depth in the mineral soil, cementing soil particles together. Various types of hardpans are described in the soil science literature, including placic horizons, plinthite layers, and duripans. Hardpans impede the drainage of water through the soil profile, resulting in a perched water table and prolonged soil saturation. Ericaceous litter decomposition rates are slow at the outset due to the abundance of polyphenols, lignin and other recalcitrant compounds, but intermittently anaerobic conditions due to waterlogged soils slow them still further. Many shrubs in the heath family are able to tolerate prolonged soil saturation (Reed, 1988) as well as the sluggish release of nutrients from soil organic matter.

Another source of shrubland stability in sites capable of supporting forest is the “frost-pocket” phenomenon (Hough, 1945; Clarke, 1946; Schlegel and Butch, 1980; Aizen and Patterson, 1995). In certain shrub-dominated depressions, invasion by forest trees is inhibited even in the absence of fire. A frost pocket starts with high-intensity wildfire or a logging operation removing the tree canopy. Heat absorbed by the ground during the day is re-emitted at night as infrared radiation, which escapes into space unless it is reflected back by tree canopies or clouds. With only a shrub cover, radiative cooling at the ground surface

is less impeded on clear nights. Swales and saddles, sometimes so subtle that they are nearly imperceptible, act as conduits for cool air drainage. The result is unseasonable frost in June, July and August. Tree seedlings, scrub oak, and most other non-ericaceous shrubs are killed or stunted or leaf-out is delayed. Late budbreak can increase susceptibility to insect herbivory (Aizen and Patterson, 1995). In the Pocono mesic till barrens, observations over several years indicate that sheep-laurel, rhodora and several lowbush blueberry species are tolerant, and scrub oak and the seedlings of red maple and most other hardwoods are highly sensitive. One 4 ha heath barren in a topographic saddle on the southern Pocono Plateau, next to a forester residence and fire tower and thus under close observation for many years, has persisted with a low, tundra-like dwarf shrub cover for at least 64 years without fire or other disturbance (1938–1939 aerial photographs; D. Miller, personal communication).

6. The role of fire

Another shrubland “stabilizer”, possibly the most crucial, involves fire. The feedback aspect stems from the co-occurrence, in many of the dominant shrubs, of two sets of traits. One set confers the means to survive even high-intensity fires, including abundant carbohydrate reserves in underground storage organs, deep rhizomes with abundant dormant buds that produce new shoots when existing shoots are damaged or destroyed, and the predominance of vegetative reproduction (Philpot, 1977; Mallik, 1993). The other set of traits confers exceptionally high combustibility to aboveground biomass and litter. It includes a high surface-to-volume ratio, high dead-to-live tissue ratio, fine branches close to the ground, high litter resistance to decomposition, low water-absorbing and water-holding capacity of surface litter, and abundant flammable compounds in foliage and bark, including terpenes, other oils, phenolics and waxes (Philpot, 1977; Williamson and Black, 1981; Bowman and Wilson, 1988; Rebertus et al., 1989; Van Wilgen et al., 1990; Gibson et al., 1999).

The fuel quality of the mix of shrub species in the Pocono mesic till barrens is so high that long-time residents refer to them in the aggregate as “kerosene bush”. Many forests in the region are highly resistant

to fire, for example, northern hardwoods, which are called the “asbestos forest” by some fire-control personnel (Lorimer, 2001). Other forests are subject to infrequent, often low-intensity ground fires, for example, oak, oak–chestnut and oak–hickory forests (Abrams, 1992). By contrast, in shrublands dominated by shrub oaks, members of the heath family, or dwarf pitch pines exhibiting shrub morphology, ignitions are much more likely to spread into high-intensity crown fires (Latham et al., 1996; Gibson et al., 1999). Some ecologists have termed highly flammable plant assemblages pyrogenic (Bond and Midgley, 1995; Zedler, 1995). High-intensity fires are unusual in northeastern forests but when they do occur, they are often high in severity; in other words, crown fires are typically lethal to forest trees. Smoldering fire in the forest duff (litter and humus), likely only during extreme drought, kills trees by burning roots and girdling the trunk cambium. In shrublands dominated by fire-tolerant species, high-intensity fires are common but, in contrast to forest fires, they are usually low in severity, that is, they generally do not kill the dominant shrubs. Aboveground parts are destroyed but roots and below-ground buds are well protected by the thick, highly absorbent and usually moist layer of recalcitrant organic matter. However, smoldering duff fires during extreme drought may be just as lethal to otherwise fire-tolerant shrubs as they are to forest trees. Before the advent of fire suppression, high-severity fires were known to smolder for days during rare prolonged droughts on the southern Pocono Plateau (e.g., Anonymous, 1908). In theory, it is these catastrophic disturbances that allow a switch between the forest and shrubland community states (Wilson and Agnew, 1992; Petraitis and Latham, 1999). A duff-reducing fire exposes mineral soil and depletes soil organic matter, degrading soil moisture-holding capacity and nitrogen pools. The trajectory of succession that follows depends on the sequence of species establishment. Initial species composition, in turn, depends on the time of year of the severe disturbance, that year’s seed production, proximity of seed sources, vectors of seed dispersal, and the weather during critical phases of post-disturbance seedling establishment.

Thus, moist-temperate shrublands most likely arise and persist as a result of historical disturbances, principally fires ignited by humans. However, the importance of fire history does not rule out plant-

induced changes in the environment as a major contributing factor in the advent and persistence of mesic shrublands where the prevailing vegetation is forest. The dominant plants in mesic shrublands, their organic residues, and their microbial symbionts differ sharply from those in forests in several key traits, notably fire sensitivity, flammability, and nitrogen relations. In theory these distinctions may give rise to different sets of feedbacks in shrublands and forests, which alter or sustain soil nutrient dynamics and fire regimes in opposite ways (see Fig. 5 in Petraitis and Latham, 1999, p. 437). Furthermore, fire history and nitrogen cycling are linked. In part, this is because severe fires volatilize and reduce total ecosystem nitrogen (Raison et al., 1984; McNaughton et al., 1998). More importantly, fire tolerance in plants is often part of a syndrome of traits that includes high nitrogen-use efficiency and decay-resistant litter with slow nitrogen release (Chapin et al., 1993), and repeated low- or moderate-severity fires can result in dominance by species possessing these traits (Ojima et al., 1994).

Records of modern fires in the northeastern United States seldom attribute ignition to lightning. Lightning in east-central North America is usually accompanied by heavy rainfall and is unlikely to ignite spreading wildfires except during severe droughts (Loope and Anderton, 1998). Trees in northeastern forests not infrequently show signs of past lightning strikes, which suggests that such events often result in just the partial burning of a single tree. Aside from the soaking that temperate deciduous forests receive in thunderstorms, even when dry their biomass makes a poor fuel, with the exception of forests with abundant oaks (Abrams, 1992).

There is stratigraphic evidence for abrupt changes in fire regime and vegetation dating from various periods before European contact at scattered locations across eastern North America (see reviews in Patterson and Sassaman, 1988; Clark and Royall, 1996; Delcourt and Delcourt, 1997, 1998). Unless independent evidence is found linking the timing of each of these changes to a localized climate shift, a more parsimonious explanation is that humans adopted fire as a landscape management tool at different times and in certain places, corresponding with areas of cultural influence. It is well documented that American Indians wielded fire over vast areas at the time of first

European contact (Day, 1953; Whitney, 1994). It is probable that Native Americans deliberately burned certain northeastern shrublands to enhance blueberry and huckleberry production or for other reasons, for hundreds or even thousands of years before European settlement (Lorimer and White, 2003).

Burning by people is most likely an essential cause of the extraordinarily long persistence times of those fire-dependent shrublands that existed before European settlement and still exist today. Equally fundamental is the succession-inhibiting effects of the particular shrub species whose fire tolerance allowed them to become dominant. If they persisted for centuries or thousands of years, fire-maintained shrublands must have bridged chance periods of prolonged wet weather or historical lapses in the practice of setting fires. Such interruptions in the fire regime, increasingly probable over longer time scales, would have allowed the replacement of shrublands on mesic soils by burn-resistant forests if it were not for additional factors retarding invasion by trees.

A key question for understanding and conserving fire-maintained communities is how long they can be expected to persist in the absence of fire. In the Pocono barrens, analyzing the historic spatial distribution of shrublands and detailed fire records has shown that the average fire return intervals for persistent shrublands before the advent of fire suppression were approximately 9 years for scrub oak barrens and 18–26 years for shrublands dominated by ericaceous species, mainly *K. angustifolia*, *Rhododendron canadense*, and *Vaccinium angustifolium* (Latham, unpublished data). In Newfoundland, *K. angustifolia* cover has been estimated to inhibit forest invasion for 40–60 years but cover by another ericaceous shrub, *Ledum groenlandicum*, delays the start of forest succession for only 6 or 7 years (Inderjit and Mallik, 1996a). Between-fire longevity of fire-maintained communities varies with species composition, climate, and other local conditions and depends on the regeneration mode, litter quality, and effects on soil of the dominant shrubs, as well as the invading species' root architecture and tolerance of the biotic and abiotic soil environment (Mallik, 1995, 2001). Methods of estimating the fire return interval required for the long-term persistence of various fire-tolerant species assemblages also vary widely among investigators and among particular research projects. Thus far, no one

has attempted a comprehensive compilation of longevity estimates for fire-maintained communities, but such an effort would be a valuable contribution to fire ecology and biodiversity conservation.

7. Debate on the fit of fire in the positive feedback paradigm

Whether the alternative community states hypothesis applies to long-lived mesic shrublands in east-central North America depends partly on the existence of a strong link between traits of the dominant species and the likelihood of wildfire. At high densities, plants that are both fire-tolerant and highly combustible increase the probability that an ignition will spread; their presence strongly influences fire behavior. Where such plants are sparse or absent, fires either fail to spread beyond the ignition point or, typically in forests, they burn only the uppermost litter layer (except during severe droughts), with relatively low heat output and little effect on tree crowns. Taking Pennsylvania as an example, historically, ignitions have been widely distributed in forest and non-forest vegetation. However, ignitions in shrub or grass-dominated barrens spread far more often into intense crown fires than those in forests, regardless of weather conditions (Clupper, 1991; Arabas, 1996; Pennsylvania Bureau of Forestry, unpublished data).

The idea that some plant assemblages may be dependent on wildfire and actually promote its spread was one of the earliest expressions of the concept of alternative community states maintained by positive feedbacks (Mount, 1964; Jackson, 1968; Mutch, 1970). The fire facilitation hypothesis presumes an amelioration of competition by fire. Other types of physical stress have been shown to contribute to the persistence of particular species in a similar fashion, even when they sustain chronic mortality, by simultaneously removing their principal competitors. Marine benthic communities have provided many specific examples (cited in Quinn and Dunham, 1983). Hypothetically, this generalization may apply even more strongly to fire-maintained terrestrial communities than to wave-maintained intertidal communities. Here the dominant species may actually contribute to increases in the frequency, intensity, and affected land area of the stress (wildfire) to which they, and not their

principal competitors, are resistant (DeAngelis et al., 1986; Platt et al., 1991; Wilson and Agnew, 1992).

The fire facilitation hypothesis has been criticized on the grounds that a trait conferring a small increment of enhanced flammability is unlikely to be selectively favored by fire, because a single plant possessing such a trait would not gain any survival or reproductive advantage; it takes many plants living together to carry a wildfire (Snyder, 1984; Christensen, 1985; Bowman and Wilson, 1988). However, some stress-adaptive traits may coincidentally confer higher flammability, for example, secondary compounds (conferring resistance to herbivores or pathogens) that happen to be highly flammable, or sclerophyll (protecting against herbivory or dessication) that slows litter decomposition rates, resulting in high fuel loads. Combinations of such traits may not decline in a population despite the increased likelihood of burning if the fitness cost of each trait is outweighed by the benefit. In other words, traits conferring high flammability need not be selected by flammability per se (Snyder, 1984). On the other hand, the models of Johnson and Boerlijst (2002) on the evolutionary implications of spatial-self structuring in multispecies systems may give new life to the idea that flammability could be selectively favored under a certain set of conditions. Others have discussed selection on fuel-quality traits as a possible explanation for the pygmy pitch pines of the pine plains in the New Jersey Pine Barrens (Gibson et al., 1999).

8. Discussion

Although most thickets in the northeastern United States are ephemeral communities on their way to becoming forest, a few northeastern shrublands persist long enough to become homes for multiple rare species. Most of these are in areas at the two extremes of the soil moisture gradient, at the highest elevations, and exposed to marine salt spray. However, available evidence points to the pre-European-settlement origin of particular areas of shrubland where there appears to be no abiotic constraint on the establishment of forest and where disturbance rates seem inadequate to explain their apparent stability. They are rare communities with comparatively high numbers of rare species.

One such shrubland, the Pocono mesic till barrens in Pennsylvania, has been undergoing invasion at the edges in the last 40 years, almost entirely by one forest species, red maple (Thompson, 1995; Latham et al., 1997). There is evidence that the process is accelerating (Maurice et al., 1999; Maurice, 2000). It is clear from its status as the sole invasive tree species that red maple has an unusually high tolerance for the suite of conditions associated with the dominant shrubs. It is also somewhat fire-tolerant where it grows in forest stands (in the local forests most of the red maples are multi-stemmed from stump-sprouting after past fires) but the high-intensity fires typical of shrublands and the dense shade of post-fire shrub root-sprouts typically kill it off. Its advance into the Pocono mesic till barrens greatly accelerated with the introduction of effective fire suppression. The highest priority for management of this unique community is to restore periodic fire to the landscape.

The mesic shrublands and other fire-maintained ecosystems that pre-dated the arrival of Europeans in east-central North America may have been sustained long before European settlement by prehistoric intentional burning (Patterson and Sassaman, 1988; Clark and Royall, 1996; Delcourt and Delcourt, 1997, 1998). Native Americans used fire most likely to improve game habitat, make hunting easier, and encourage the growth of certain fire-enhanced sources of foods such as blueberries and huckleberries. It is possible that cultural change may have brought intentional wildland burning to various areas in east-central North America at different times. For example, in a 9000-year chronology from a sediment core collected from a swamp next to the Shawangunk Mountain shrub-dwarf pine barrens, Laing (1994) showed a sudden increase in fire activity 1920 ± 50 years ago followed by sustained high levels to the present. This was inferred from an upsurge and subsequent plateau in charcoal values and percentages of pollen from pitch pine and Ericaceae, components of the shrubland community that still occupies the site.

Long-lived shrublands in the northeastern United States (e.g., sandplains, dune thickets, alpine communities, and peatlands) stir scientific and esthetic interest as anomalous landscapes and as habitats for unusual clusters of rare species. But part of the value and appeal of the mesic shrublands and pine plains, in particular, also may be cultural, historic and anthropological.

Despite their wilderness aspect they may be, in a sense, artifacts, part of our cultural heritage. It is likely that such habitats existed in greater abundance before European settlement, but only a few happened to undergo continued disturbance by European immigrants in a manner similar enough to the old disturbance regime to enable the dominant shrubs, and the subordinate rare species, to persist. Thousand-year-old anthropogenic shrublands share the distinction of abundant rare plant species with sandplains, calcareous fens, alpine tundra, and salt-spray thickets. Those of Native American origin may be even older in some cases, owing to high rates of erosion on mountaintops and shifting dunes on the seacoast. Much more palynological study will be needed before this conjecture can be confirmed or refuted.

To carry the “ancient artifact” analogy a step further, any prehistoric Indian-maintained shrublands that still exist in the northeastern United States have been the subjects of active preservation and maintenance, however inadvertently, by Westerners ever since they replaced Native Americans as stewards of the land. Government agencies and conservation groups like The Nature Conservancy have made stewardship of such places intentional by naming some of them as high in priority for biodiversity conservation. Experimental and historical research addressing key unanswered questions, including those posed in this paper, is needed to put shrubland conservation in the northeastern United States on a sound footing and to insure the continued longevity of these extraordinary ecosystems.

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