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A comparison of floristic diversity in old-growth versus mid-successional secondary-growth hardwood forests of the White Mountain National Forest, New Hampshire, United States

Leslie Marie Teeling-Adams
University of New Hampshire, Durham

A COMPARISON OF FLORISTIC DIVERSITY IN OLD-GROWTH VERSUS MID-SUCCESSIONAL SECONDARY-GROWTH HARDWOOD FORESTS OF THE WHITE MOUNTAIN NATIONAL FOREST, NEW HAMPSHIRE, USA

BY

LESLIE M. TEELING-ADAMS
B.S., University of New Hampshire, 1993
M. S., University of New Hampshire, 1998

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300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

This Dissertation has been examined and approved.

Dissertation Director, Dr. Garrett E. Crow
Professor of Botany
Chair Person, Department of Plant Biology

Dr. Thomas D. Lee
Associate Professor of Natural Resources

Dr. Christopher D. Neefus
Professor of Plant Biology and Biostatistics

Dr. Janet R. Sullivan
Affiliate Associate Professor of Plant Biology

Dr. Gary L. Wade
USDA Forest Service Ecologist

5 May 2003
Date

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ABSTRACT

A COMPARISON OF FLORISTIC DIVERSITY IN OLD-GROWTH VERSUS MID-SUCCESSIONAL SECONDARY-GROWTH HARDWOOD FORESTS OF THE WHITE MOUNTAIN NATIONAL FOREST, NEW HAMPSHIRE, USA

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There is currently debate over whether managed forests will ever regain the species diversity of old-growth stands. While succession and response to disturbance of tree species has been extensively researched, little similar effort has focused on understory herbaceous communities. This study conducted large-scale, comprehensive botanical inventories of three old-growth and three mid-successional (80-100 year old) secondary forest stands in New Hampshire's White Mountain National Forest (WMNF). Cluster analysis and TWINSPAN grouped the secondary sites within two steps. Old-growth floras were significantly richer in total, total herbaceous, woodland herbaceous, and unique herbaceous species. Abundance distributions of the two treatment groups were significantly different according to Chi^2 results: more woodland herbaceous species of rare, infrequent, or dominant abundance rank occurred in old-growth sites. Floristic similarities were analyzed using Sørensen's Index of Similarity. Tree community data did not reflect differences in floristic diversity, suggesting that reliance on tree data alone to infer system recovery from disturbance would be misleading.

Key words: diversity, forest ecosystem, flora, old-growth, recovery, succession, clearcutting

INTRODUCTION

Old-growth forest ecosystems in the northeastern United States have been substantially altered by human forces. Fragmentation, pollution, silvicultural activities, changes in hydrology and microtopography, and the suppression or elimination of fires and large carnivores exert new pressures on forests that had been largely undisturbed, perhaps since the end of the Pleistocene (Braun 1950). Although the variability of "old-growth" definitions and the scattered distribution of these areas across public and private lands have resulted in difficulty estimating the number of acres remaining nationally (Heinz Report 2002), the scientific value of these areas is undisputed. Forest ecosystems untouched by human development and silviculture have the potential to function as genetic source pools, and may be critical to the enrichment of recovering systems (Matlack 1994). They represent what Aldo Leopold (1972, pp. 145 - 146) referred to as "*the base datum of normality.*"

Relatively free from human influence, pre-settlement mesophytic forests of the eastern U. S. and Canada experienced infrequent catastrophic disturbance and likely constituted one of North America's least disturbance-prone forest types (Davis 1996). Even today, fire and hurricane damage tend to have greater impact near the edges of eastern deciduous forests, and the effects of such events are often small in scale. Much more common to disturbance regimes in these systems are individual or small-scale treefalls, resulting in canopy gaps (Bormann and Likens 1979; Davis 1996; Kimball et al. 1995; Kimmins 1997; Tyrrell and Crow 1994; Runkle 1982). Given the natural pattern of

stability in these forest systems, researchers have expressed concern over the ability of old-growth temperate forest ecosystems to recover from the intense disturbance of many current tree harvesting methods (Goebel et al. 1999; Halpern and Spies 1995; Meier et al. 1995; Roberts and Zhu 2002; Spies 1991; Teeling 1998; Teeling et al. 2001).

Scientific interest in the effects of species diversity on natural systems continues to intensify with reports of escalating species extinctions worldwide (Christensen et al. 1996; Doak et al. 1998; Tilman and Downing 1994; Wilson 1992). While there is debate over the exact mechanisms, the basic hypothesis that diversity adds to the stability of ecosystems has fostered renewed interest in diversity theory in recent years (Doak et al. 1998; Grime 1997; Hooper and Vitousek 1997; Naeem et al. 1995; Tilman and Downing 1994; Tilman et al. 1997, 1998). Conceptual models attempting to explain temporal and spatial patterns of species diversity in temperate forests abound; richness has been related to successional age, disturbance, competition, productivity, resource and habitat heterogeneity, nutrient dynamics, predation, positive interactions, population growth rates and life-history strategies (Bormann and Likens 1979; Connell 1978; Grime 1973,1979; Hacker and Gaines 1997; Halpern 1989; Halpern and Spies 1995; Huston 1979; MacArthur and Wilson 1963; Petratitis et al. 1989; Roberts and Gilliam 1995; Rosenzweig and Abramsky 1993; Tilman and Pacala 1993; Waide et al. 1999; Whittaker et al. 1973; Williams 1964). The number of theories alone attempting to predict species richness suggest that a complex pattern of interrelated factors likely govern diversity in biological systems, and ultimately, their interplay may be system-specific.

The maintenance of species diversity is an important directive of USDA Forest Service's management policy (Christensen et al. 1996; Fay, pers. comm.; Roberts and

Zhu 2002; Wade pers. comm.). In temperate hardwood forests, herbaceous species comprise the predominant component of the flora, often representing upwards of 70% of species (Bormann and Likens 1979; Leak 1987; Siccama et al. 1970; Teeling 1998; Teeling et al. 2001; Westveld et al. 1956). Diversity in this community therefore exerts critical influence on the system's floristic diversity overall, yet the effects of today's silvicultural practices on forest floor communities are still not well-understood (Goebel et al. 1999; Halpern and Spies 1995; Johnson et al.1993; Meier et al. 1995; Roberts and Zhu 2002; Teeling et al. 2001). The preponderance of ecological data from New England forests has historically focused on tree species alone, with understory species examined only in terms of biomass or percent cover. While the number of understory studies has increased over the last few decades, focus has typically been limited to only a few dominant species or categories of species. It is only very recently that studies attempting to address full floras, including herbaceous species, have begun to appear in the literature. The result of this gap has been that while succession, diversity patterns and response to disturbance in the tree layer have been well-understood for some time, our understanding of similar processes in herbaceous communities remains largely theoretical (Halpern and Spies 1995; Johnson et al. 1993; Meier et al. 1995; Roberts and Zhu 2002). Hence, speculation continues in the scientific literature as to the long-term effects of silvicultural practices, but we as yet have few clear answers (Bratton 1976; Carbonneau 1986; Meier et al. 1995; Teeling 1998; Teeling et al. 2001; Whitney and Foster 1988).

On average, 770 ha of the White Mountain National Forest of New Hampshire (or about 0.5%) are projected for harvest annually. Clearly, intensive logging represents a catastrophic disturbance to any forest system and has the potential to drastically alter

species composition directly through loss of the canopy, and indirectly by reverting the system to an earlier successional stage (Bormann and Likens 1979). Large-scale loss of the canopy increases solar radiation reaching the forest floor dramatically, which in turn elevates soil temperature and decreases soil moisture. The initial physical impacts of harvesting include the uprooting and trampling of understory vegetation by equipment, soil compaction, redistribution of the forest floor, disruption of the seed bank, changes in nutrient dynamics, rutting and erosion (Bormann et al. 1974; Bormann and Likens 1979; Mou et al. 1993; Pierce et al. 1993). Canopy removal initiates a period of intense competition between forest floor species and shade-intolerant, or ruderal species (*sensu* Grime 1973), while the stand reinitiates itself. A period of "stem exclusion" follows (*sensu* Bormann and Likens 1979) as the canopy closes and self-thinning of overstory trees commences. Tree mortality during this stage often causes no gap in the canopy, or only small gaps that close rapidly, and species diversity in the understory declines sharply due to the reduction of penetrating solar radiation. As the overstory matures, a transition phase begins in which self-thinning continues, but gaps are larger and slower to close. It is during this stage that increased solar radiation penetrates the canopy to the forest floor, permitting understory re-establishment and, theoretically, allowing system diversity to increase to pre-cut levels (Bormann and Likens 1979).

Thus far, however, there has been little empirical evidence from studies of recovering secondary-growth forests in support of this classical recovery theory. Part of the problem has been the lack of floristic data from old-growth forests, our "base data of normality." While a number of studies have indicated that diversity may remain lowered even 70 to 90 years after harvest (Clebsch and Busing 1989; Duffy and Meier 1992;

Gilliam et al. 1995; Matlack 1994; Teeling et al.2001; Roberts and Zhu 2002), only two studies comparing floristic diversity in old-growth and mid-successional secondary-growth forests of the eastern U. S. appeared prior to this study. Duffy and Meier (1992) compared the diversity of nine old-growth and nine environmentally similar secondary forests (45 to 87 years old) of the southern Appalachian and Cumberland Mountains. Their study found secondary forest floras both significantly less rich and less abundant (in terms of species population sizes), with no evident trend toward recovery of either variable. While this study has been criticized by some (Duffy 1993; Elliott et al. 1993; Johnson et al. 1993), Goebel et al. (1999) reported similar findings in their study of two old-growth and two 70-79 year old, previously cut mixed *Quercus* forests of southeastern Ohio. Using canonical correspondence analysis (CCA), their study found old-growth floras more abundant and significantly richer than secondary floras in early spring, late spring and mid-summer herbaceous flora. Thickness and pH of the soil A horizon and stand age demonstrated the highest influence on species diversity.

The study presented here sought to further investigate floristic differences between old-growth and secondary-growth forest floras and constitutes the first comparative study of its kind in New England. While Whitney and Foster (1988) compared understory and overstory species of old-growth and secondary old-field hardwood forests of Massachusetts and southern New Hampshire, they did not examine diversity. Crow et al. (1994) and Royte et al. (1996) performed detailed botanical reconnaissance of two old-growth preserves (Mountain Pond Research Natural Area (RNA) and Nancy Brook RNA, respectively), but did not compare their findings with secondary systems. Carboneau and Allen's (1995) botanical reconnaissance of the Bowl

RNA did not collect adequate data for comparisons. Teeling et al. (2001) conducted complete botanical inventories of the experimental watersheds of the Hubbard Brook Experimental Forest, constituting close to 350 ha of mid-successional secondary or young tertiary forest, but did not compare these data to old-growth floras.

The method of the study presented here was also unique. Full botanical inventories were conducted of large, representative areas of the sites under examination rather than employing plot-based sampling techniques. Although exceedingly rare, full-inventory studies yield the most comprehensive data for the assessment of species diversity. Plot-based methods lend increased risk of missing rare species, which have been theorized to be among the better indicators of primary systems (Halpern and Spies 1995; Meier et al.1995; Peterken and Game 1984; Roberts and Zhu 2002; Rooney and Dress 1997; Spies 1991; Whitney and Foster 1988). Studies employing plots also have the tendency to underestimate the abundance of species with contagious distributions, making them problematic in the study of old-growth forests where many species propagate clonally (Kimmins 1997; Mueller-Dumbois and Ellenberg 1974; Sobey and Barkhouse 1977; Whitford 1949). The intensive investment in field time required for full inventories yields comprehensive, fine-grained data best suited for diversity studies and long-term monitoring of floristic composition.

The objectives of this study were to 1) conduct comprehensive botanical inventories, with abundance estimates, of 7 ha representative sections of three old-growth hardwood forest preserves in the White Mountain National Forest, thus providing baseline floristic data for their long-term monitoring, 2) determine floristic variation between these old-growth sites and three 80-100 year old environmentally similar

secondary forest sites with respect to total, tree, herbaceous, vernal, spring ephemeral, and woodland herbaceous species, 3) determine floristic variation between these old-and secondary-growth sites with respect to species associated with wet, moist and/or rich and dry and/or disturbed forest soils 4) determine the variation in species abundance patterns between old-growth and secondary sites with respect to total, tree, herbaceous, vernal, spring ephemeral, and woodland herbaceous populations, and 5) to theorize the basis for any observed differences between these two forest types.

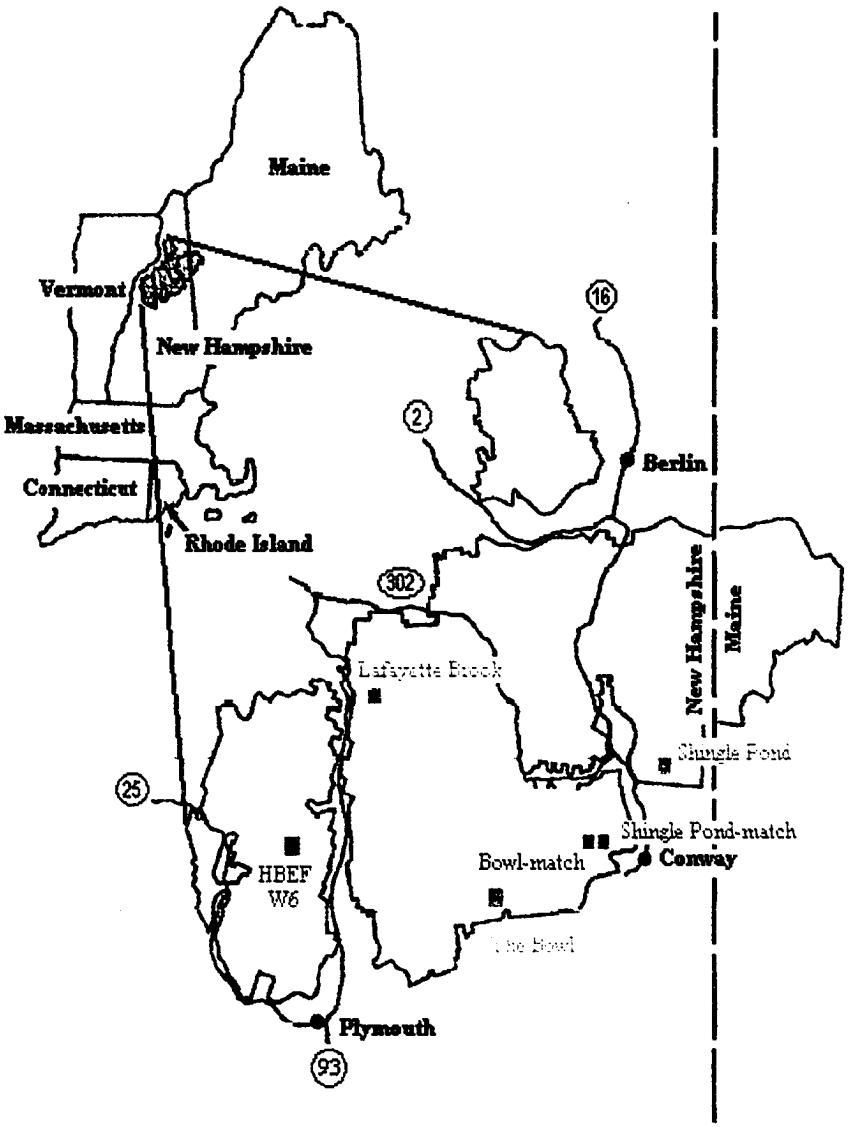
Differences in the vernal herbaceous flora and spring ephemeral flora (a subset therein) were explored in response to questions specifically regarding these species that are still outstanding in the scientific literature (Duffy and Meier 1992; Goebel et al. 1999; Meier et al. 1995).

SITE DESCRIPTIONS

Established in 1911, the White Mountain National Forest is composed of almost 800,000 hectares of New Hampshire and western Maine (Figure 1). Three sites in old-growth hardwood forest and three sites in mid-successional secondary-growth hardwood forest were inventoried for this study. The sites classified as old-growth forests have a history of use by earlier researchers (Bailey and Cogbill, submitted; Carbonneau 1986; Cogbill, unpubl. data.; Goodale 1999; Leverett 1966; Martin pers. comm.), and met the functional, structural and historical criteria specified by this study, as follows:

1. the presence of self-replacing, predominately shade-tolerant or late successional tree species in the canopy
2. a tree community with a diversity of age classes (that is, having a multi-layered canopy), including the presence of some trees near the end of their natural lifespan
3. large standing dead trees (snags) and large decaying logs commonly occurring throughout the stand
4. a history or evidence of a long, uninterrupted period of development, substantially free of significant human or natural disturbance such as catastrophic logging, fire or hurricane damage
5. canopy gap-phase dynamics commonly occurring throughout the stand; a "patchiness" of both microtopography and canopy structure indicative of small-scale disturbances, such as the downing of individual large trees

Figure 1. Locations of the six study sites in the White Mountain National Forest, NH.



"Hardwood forest" was defined as having a combined presence of no more than 10% coniferous species in the canopy. Typical northern hardwood forest composition in these sites was characterized by a dominant presence of *Fagus grandifolia*, *Acer saccharum*, and *Betula allegheniensis*, with less abundant populations of *A. pensylvanicum*, *A. rubrum*, *Picea rubens*, *Abies balsamea*, and *Tsuga canadensis*. Understory vegetation was abundant and largely dominated by *Viburnum alnifolium*, with herbaceous species such as *Erythronium americanum*, *Maianthemum canadense*, *Dryopteris intermedia*, *Aster acuminatus*, and *Uvularia sessilifolia* commonplace on the forest floor.

Geographical Information System (GIS) data, provided by the Pemigewasset Forest Service Station in Laconia, NH, were used to identify two of the three environmentally similar secondary forest sites used as matches for old-growth sites. The four coverages used were the Forest Service's Ecological Land Type (ELT) classification system, minimum stand age, minimum stand area, and land use history (provided by Dr. Christine Goodale of the Woods Hole Research Center in Woods Hole, MA; unpubl. data). The ELT classification system categorizes land based on vegetation type, soils and geomorphic processes; site climate, elevation, slope aspect and bedrock types are therefore inherent. The Forest Service's GIS database was queried for sites within the White Mountain National Forest (WMNF) with 1.) ELTs corresponding to old-growth sites, the Bowl and Shingle Pond, 2.) a minimum stand age of 80 years, and 3.) a minimum stand area of 20 hectares. Results were then cross-referenced with the land use data to select sites which also had a history of heavy hardwood logging in the early 1900s. Forest Service records were checked to insure potential sites were not impacted by

the 1915 Paugus-Pasaconawway fire, and ground reconnaissance was used to further select the best secondary-growth matches for two of the three old-growth sites.

An environmentally similar secondary-growth site was chosen for the third old-growth site, Lafayette Brook, using separate sources of vegetation, soils, topographic and land use history data, as explained in the secondary-growth sites descriptions (page 19).

Old-Growth Sites. The Bowl Research Natural Area (RNA) is located in Campton, New Hampshire, in the Sandwich Range Wilderness Area of the WMNF. It encompasses approximately 206 ha of the western drainage area of the West Branch of the Wonalancet Brook and includes most of the eastern slope of Mount Whiteface. Elevations range from 620 to 1215 m. Mean monthly temperatures range from -10°C in January to 17.2°C in July, with the frost-free growing period averaging around 95 days (Carbonneau and Allen 1995). Mean annual precipitation is approximately 145 cm, with 4.2 m mean annual snowfall. The Bowl has a long history as a valuable old-growth research site. As such, tree harvesting is prohibited, forest fires are suppressed and no hiking trails traverse the RNA, though it is accessible from several WMNF's trails. Northern hardwood forest is present at lower elevations, while mountain spruce-fir forest predominates over most of the western portion of the RNA, rising toward the summit of Mt. Whiteface.

An 8.1 ha study site was delineated along the southern section of the brook in the hardwood forest at an elevation of approximately 620 to 670 m (Table 1; Figure 2). The site is east-facing in aspect and terrain was typically steep, with slopes anywhere from 0° to 35°. Soils in this region are classified only as "rough mountainous land" by the USDA's Soil Survey, a designation broadly encompassing podzolic soils of the rough

Table 1. Defining coordinates for the six study sites, expressed in degrees and minutes.

The Bowl	Shingle Pond	Lafayette Brook	Bowl-match	Shingle Pond-match	HBEF W6
N43° 55.871	N44° 05.623	N44° 10.809	N44° 0.738	N44° 0.813	N43° 56.981
W71° 23.193	W71° 04.249	W71° 40.977	W71° 15.623	W71° 14.617	W71° 44.233
N43° 55.914	N44° 05.739	N44° 10.773	N44° 0.815	N44° 0.947	N43° 57.038
W71° 23.205	W71° 03.345	W71° 40.834	W71° 15.440	W71° 14.517	W71° 44.373
N43° 55.972	N44° 05.741	N44° 10.845	N44° 0.823	N44° 0.949	N43° 57.162
W71° 23.212	W71° 04.234	W71° 40.927	W71° 15.344	W71° 14.452	W71° 44.498
N43° 56.038	N44° 05.700	N44° 10.932	N44° 0.779	N44° 0.741	N43° 57.303
W71° 23.132	W71° 03.016	W71° 41.185	W71° 15.251	W71° 14.434	W71° 44.609
N43° 56.050	N44° 05.633	N44° 10.953	N44° 0.661	N44° 0.736	N43° 57.314
W71° 23.304	W71° 03.994	W71° 41.078	W71° 15.612	W71° 14.567	W71° 44.530
N43° 56.108					N43° 57.332
W71° 23.309					W71° 44.462
N43° 55.895					N43° 57.239
W71° 23.231					W71° 44.426
					N43° 57.108
					W71° 44.340

Figure 2. Study site within the Bowl Research Natural Area, Campton, NH.

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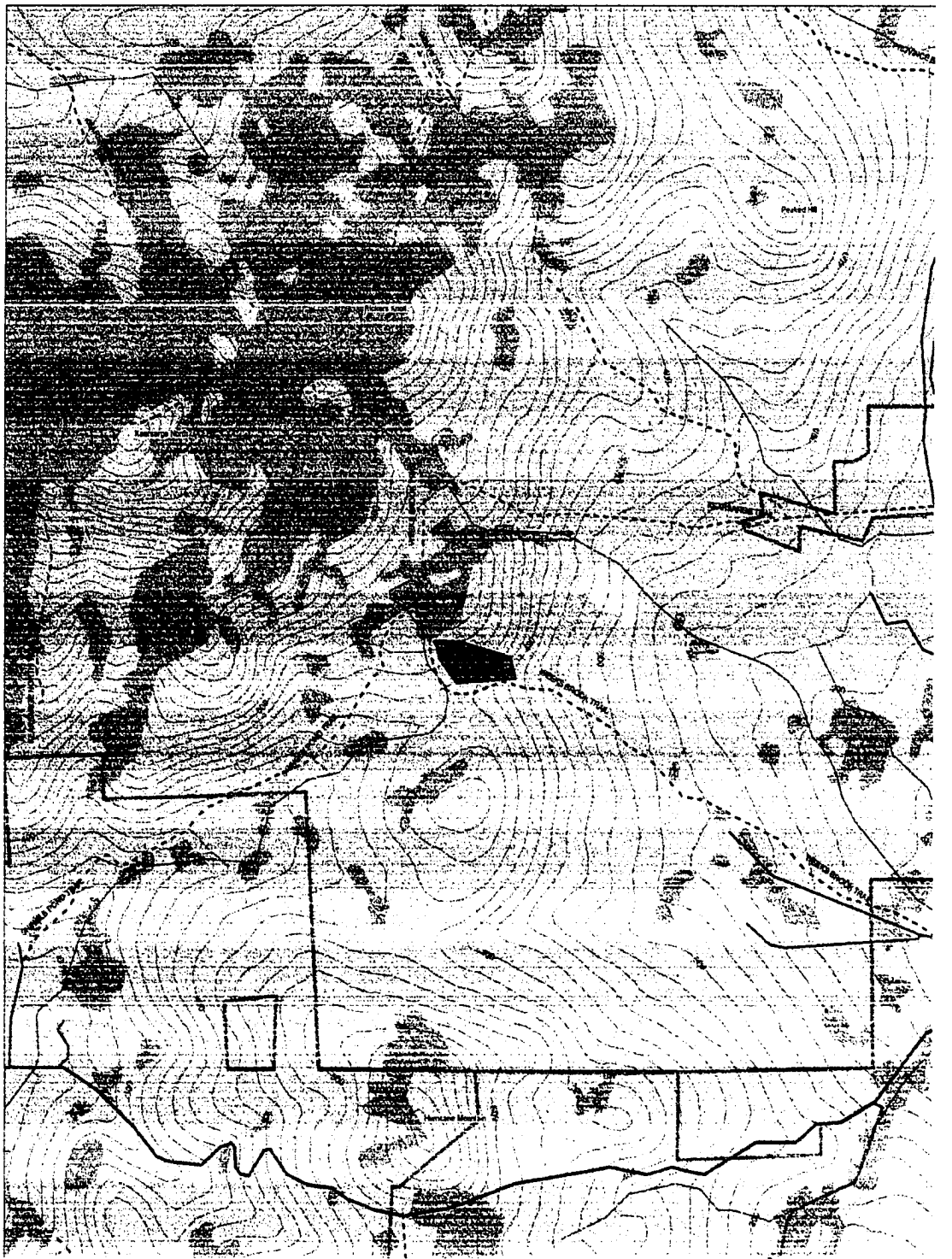
and stony land group (Latimer et al. 1939). However, research conducted by USDA Forest Service Geologist Scott Bailey at the Hubbard Brook Experimental Forest Research Station more finely characterizes the study site soils as Berkshire series sandy loams and Monadnock series loamy sands (unpubl. data). Soil depths reached 2 meters, although a densipan layer also was found in one location at a depth of approximately 29 inches. This area encompassed many vernal drainage streams, two perennial streams and a series of flat seeps characterized by a diverse flora.

The area surrounding Shingle Pond (SP), located in the WMNF of Intervale, New Hampshire, is presently considered a candidate RNA. Northern hardwood forest is present at lower elevations, while mountain spruce-fir forest predominates over most higher elevations. A 7.2 ha study site was delineated approximately 2 km southeast of the pond, along the Weeks Brook Trail (Figure 3). Elevations ranged from 225 to 265 m, with slopes from 0^{o} to 15^{o} in a southeasterly direction.

Soils in this region are classified as Monadnock series loamy to gravelly sand (Bailey, unpubl. data). Lyman soils likely predominate on rocky outcrops and shallow ledges, and Peru soils in drainage ways and wetter areas (USDA Soil Conservations Service and Forest Service 1977). A hiking trail forms a boundary along the area's southern border, necessitating a setback of the site 10 meters to avoid floristic edge effects. While relatively flat in gross topography, the Shingle Pond study site encompassed many microhabitats (defined here as a physical and/or resource niche supporting a distinctive subset of the larger flora) by virtue of its complex system of perennial and vernal streams, wet seeps and extensive canopy gaps.

The Lafayette Brook Scenic Area (LB), located in the WMNF in Franconia, New

Figure 3. Study site near Shingle Pond, Intervale, NH.



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Hampshire, is a 47 ha tract of land off the northwest slope of Mount Lafayette. The forest is a mix of northern hardwood and mountain spruce-fir types. A 5.6 ha study site was delineated off the eastern side of Interstate 93, near the northern end of Franconia Notch State Park (Figure 4). Elevations ranged from 560 to 620 m, with slopes from 0° to 20° in a northeasterly direction. Meteorological records kept by the Cannon Mountain Valley Station reported a mean January temperature of -8.5° C, and a mean July temperature of 17.8° C for the 1990s. Average precipitation in snowfall for that same period was reported as 3.02 m. A small parking lot along the area's north-eastern border necessitated a site setback of 10 meters to avoid floristic edge effects.

Soils in this region are classified as Peru series sandy loams with a pan layer composed of compacted basal till (Bailey, unpubl. data). Many vernal and perennial drainage streams, animal trails, and wet seeps provided this site with a wealth of microhabitats. While most of the forest was northern hardwood type, one large area of moss-covered boulder field existed which was dominated by nearly pure coniferous forest. In this areas, little understory existed.

Secondary-Growth Sites. Two sites along the Kancamagus Highway (NH Route 112), in Albany, NH were chosen as good environmental matches for the Bowl and Shingle Pond old-growth study sites. According to 1911 historical records, both sites were categorized as "selectively to heavily cut" stands of northern hardwood and mixed spruce-fir forest prior to their procurement by the U. S. Forest Service in 1914. This stretch of the Kancamagus Highway was constructed along the path of two former logging railroads, as well as along the banks of the Swift River, and it is therefore likely

Figure 4. Study site within Lafayette Brook Scenic Area, Franconia, NH.

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that the area was hardwood forest in the 1900s. Hardwoods were the preferred fuel to power steam engines, and railways were preferentially laid along stretches of deciduous forest. Those interested should see Belcher (1980) for a complete history.

The Bowl-match site (B-m) was a 7.18 ha tract of land at the base of Big Attitash Mountain, just south of the Kancamagus Highway. Elevation ranged from 320 to 380 m, with slopes from 10° to 35° in a north to north-westerly direction (Figure 5). Soils in this region are classified as Monadnock series loamy sands (Bailey, unpubl. data). Only one stream traversed this site. While slopes within this site varied, microtopography was observed to be particularly homogeneous in nature. Most of the forest was northern hardwood type, with some steeper portions of the site dominated by mixed hardwood-coniferous forest.

The Shingle Pond-match site (SP-m) was a 7.35 ha tract of land, also at the base of Big Attitash Mountain, just east of the Kancamagus Highway (Figure 6). Elevations ranged from 280 to 340 m, with slopes from 0° to 30° in an easterly direction. Soils in this region are classified as Berkshire series sandy loams and Monadnock series loamy sands (Bailey, unpubl. data). This site was largely flat and even in topography, except for a talus slope on the southwest border with slopes ranging up to 35°. Vegetation in this boulder-field area was almost exclusively *Acer spicatum* and *A. pensylvanicum* with little understory development. The site encompassed many vernal streams and a small perennial wet seep characterized by a diverse flora.

While B-m and SP-m were close in proximity, differences in canopy composition were judged to be significant enough during ground-proofing provide supportive evidence for their different ELT classifications and to justify their selection. The

Figure 5. Bowl-match study site in Albany, NH.

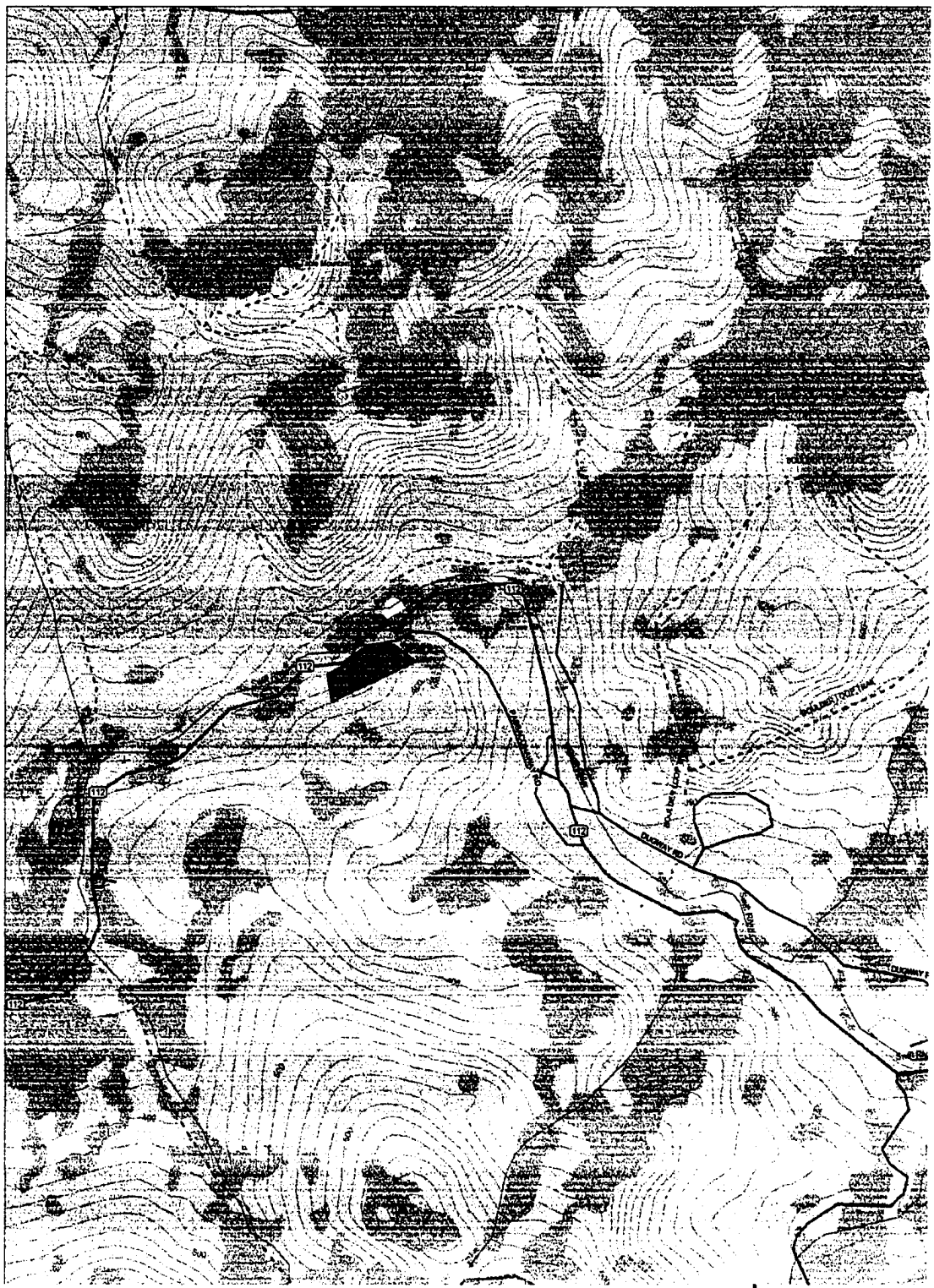

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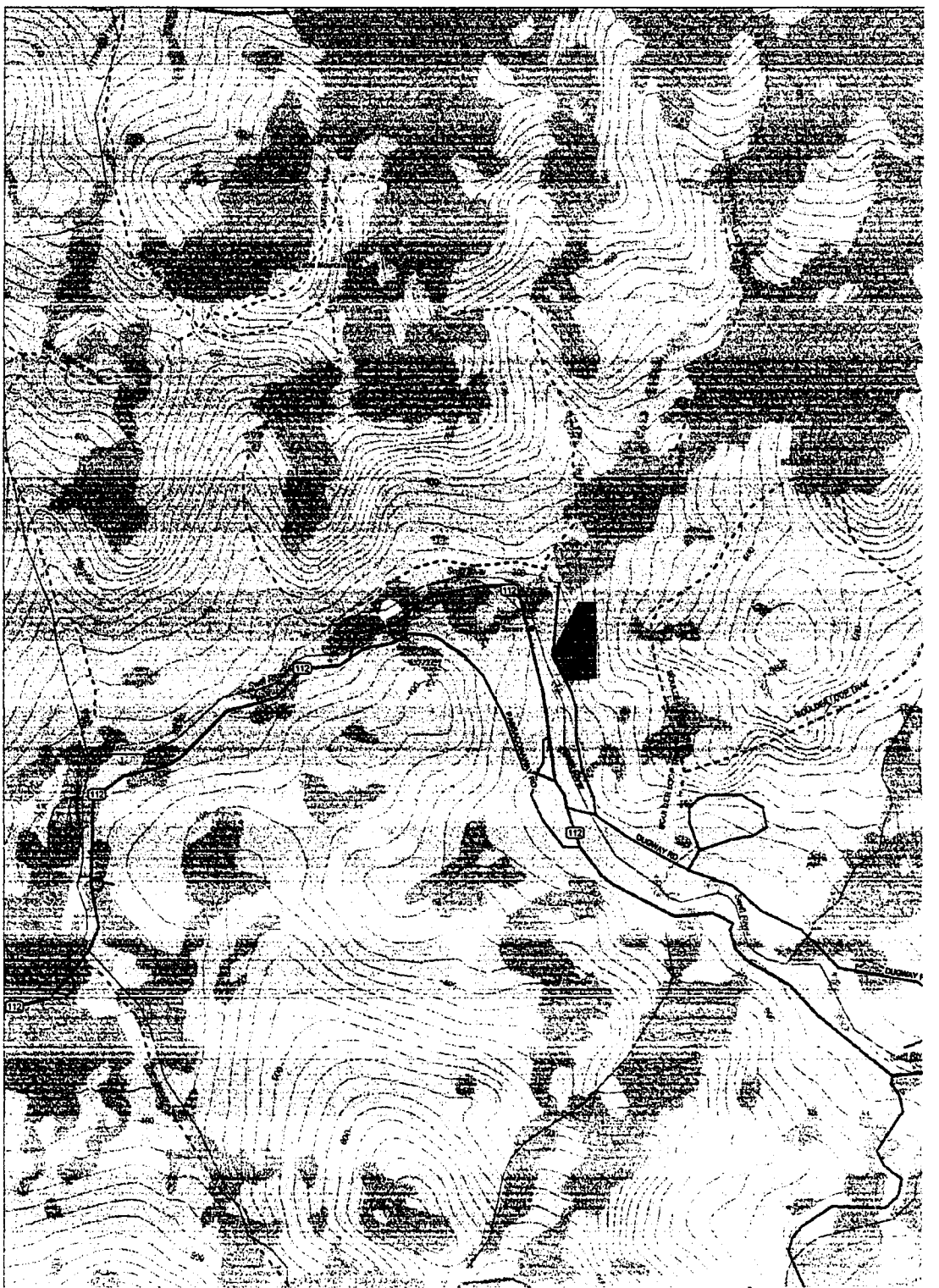
Figure 6. Shingle Pond-match study site in Albany, NH.



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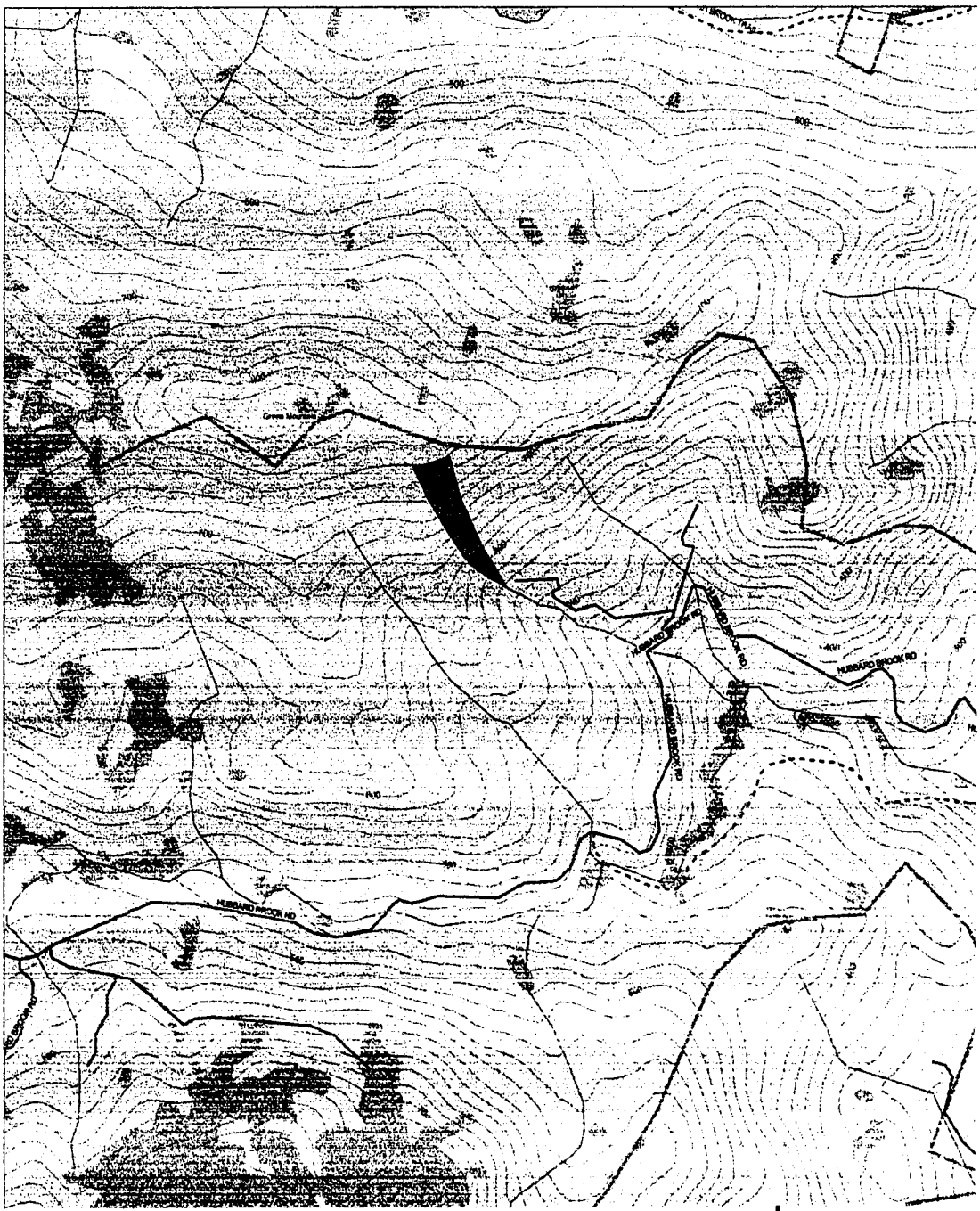
hardwood portion of Watershed 6 (W6) of the Hubbard Brook Experimental Forest (HBEF) was selected as the environmental match for the Lafayette Brook Scenic Area (Figure 7). As the HBEF is not covered by Forest Service GIS data, this selection was made using HBEF vegetation, soils, topographic and land use history data. An international Biosphere Reserve, HBEF comprises a 3160 ha portion of the WMNF in Woodstock, New Hampshire, dedicated as a Long Term Ecological Reserve (LTER), and operated by the USDA Forest Service's Northeastern Forest Experiment Station. Since the Hubbard

Brook Ecosystem Study was founded in 1963, ten small, well-defined experimental watersheds have been delineated in the northeastern section of the bowl-shaped Hubbard Brook Valley. These experimental watersheds were inventoried in the late 1990s, employing the same methods used in this study (Teeling et al. 2001).

Prior to 1895, most of the Hubbard Brook Valley was mature, primary forest (Bormann et al., 1970; Likens and Bormann, 1995). Historical records indicate that intensive logging between the turn of the century and 1917 resulted in the majority of both hardwood and coniferous tree species being removed. There has been no evidence of logging after this time, nor any evidence of subsequent fires or serious damage as a result of the 1938 hurricane (Cogsbill, pers. comm.). At the time of this study, W6 was characterized as a relatively even-aged, secondary forest with some older trees present. Its stand composition had been referred to as reasonably representative of climax and it was used most frequently used as a vegetation reference or control by HBEF researchers (For more on W6, see Bormann et al. 1970; Leak 1987; Siccama et al. 1970; Whittaker et al. 1974). Approximately 75.3% (9.9 ha) of W6's 13.2 ha is hardwood forest, the rest

Figure 7. Study site within Watershed 6 of the Hubbard Brook Experimental Forest, Woodstock, NH.



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being mixed hardwood-spruce-fir or pure spruce-fir forest. A species list for the hardwood only portion of this watershed was available from Teeling (1998), as our study inventoried watersheds by forest type. Elevation in the hardwood region ranged from 549 m to approximately 660 m, with slopes from 0^{o} to 25^{o} in a southeasterly direction. Soils in this region were classified by Siccama et al. (1970) as mainly Berkshire coarse to very stony fine sandy loams with a relatively impermeable bedrock at a depth of 0.5 to 3.0 m. This site was largely flat and even in topography, and encompassed only a few vernal streams.

MATERIALS AND METHODS

Reconnaissance field surveys were used to inventory the flora of each study site. The last weeks before the growing season began (early May) were spent mapping microhabitats and dividing the sites into segments that could be comprehensively surveyed in a field day. Each of these segments was then visited weekly from mid-May through early September and systematically walked, using compass azimuth at 10 to 20 m intervals. Watershed 6 of the HBEF was surveyed during the field seasons of 1995 and 1996. The study sites at the Bowl RNA, Shingle Pond and the Lafayette Brook Scenic Area were surveyed during the 1999, 2000, and 2001 field seasons, respectively (variations in climatic conditions during the time period field data was collected were not judged to be significantly influential on the flora). The Albany secondary forest sites were surveyed during the 2002 field season. Species lists were compiled and voucher specimens were collected for the old-growth sites, unless to do so would have threatened the existing population. Collections were deposited in the Hodgdon Herbarium (NHA) at the University of New Hampshire. No specimens were collected from W6 due to a HBEF minimal-disturbance policy for this watershed, and collections were taken from the Albany sites only in the case of difficult or potentially controversial identifications.

Estimates of species abundance within each segment of a study site were made based upon the rank abundance approach suggested by Palmer et al. (1995; Table 2). This system was used to rank the frequency of occurrence of individuals of a species in relation to the total flora, and was the same method used by Teeling et al. (2001). A

Table 2. Frequency of occurrence scale modified from Palmer et al. (1995). Species constituting approximately 20% or more of all individuals present in its community type (i.e., tree, shrub or herbaceous) were defined as "dominant" species. Ramets of clonal species were defined as "individuals."

Rank	Category	Qualitative Description
5	Abundant	Dominant or codominant in one or more common habitats.
4	Frequent	Easily seen or found in one or more common habitats, but not dominant in any.
3	Occasional	Widely scattered, but not difficult to find.
2	Infrequent	Difficult to find, few individuals or colonies, but found in several locations.
1	Rare	Very difficult to find and limited to one or very few locations or uncommon habitats.
0	Absent	Not found, but found in a previous survey from the same or similar sites, or was otherwise suspected to occur.

"dominant" species was defined as one constituting approximately 20% or more of the individuals present. Due to the prevalence of clonal species in this study, ramets were regarded as "individuals." In a highly diverse area it was therefore possible to have no species rate in the "abundant" category (5), but rather, several rated only as "frequent" (4). At the end of the field season, data from all segments of the study site were combined. The proportional area a segment represented was calculated and estimates of species abundance were averaged according to that proportion, yielding an estimate for each study site in its entirety. Teeling-Adams conducted the field work for all six sites, minimizing variations in abundance estimates.

Data were analyzed both by individual study site and by forest type (old-growth vs. secondary-growth). Resultant floras were examined in their totality, as well as compositionally by tree, shrub, and herbaceous communities. The taxonomic keys of Gleason and Cronquist (1991) and Voss (1985, 1996) make note of species with known soil and habitat associations. Species in this study were classified as reliant on 1) wet soils, 2) dry and/or disturbed soils, and 3) moist and/or rich soils, as denoted in the above two manuals. Species that were tolerant of a wide range of conditions, or for which no information was expressly given, were left without designation. Taxa which were not identified to species were also left without designation. The herbaceous community was further divided into "woodland," nonwoodland and vernal species lists. Spring ephemeral species, a subset of the vernal herbaceous flora, were also examined for some analyses.

The definition of "woodland species" used here was adapted from a Peterken and Game (1984) analysis, which partitioned "shade-casters, shade-bearers, and wood-

margin species" (p. 159) into a group seen as more representative of undisturbed forests. For this study, species of forested wetland areas (seeps, streams) were included in the woodland species list. Vernal species were defined as species flowering by early June (tho not necessarily senescing); spring ephemeral species were defined as per Rogers (1982) as species with senescence of photosynthetic shoots by early June. Unique species, defined as species occurring only in one watershed and/or one forest type, were also examined.

The study sites were hierarchically classified by species importance values, using both divisive and agglomerative methods, to investigate differences in species richness coupled with species abundance. Two-way indicator species analysis (TWINSPAN) was used to numerically classify the sites (Hill et al. 1975; Kent and Coker 1992). The total flora and various subsets therein and were analyzed separately. Ward's minimum variance clustering was used to corroborate TWINSPAN results (Pielou 1984). Both analyses were conducted using PC-ORD software, version 3.06 (MjM Software Design).

Sørensen's Index of Similarity, expressed as a proportion, was calculated for the study sites' total, tree, shrub, herbaceous, and vernal herbaceous flora, by study site. This index measures the number of coinciding species occurrences against the number of theoretically possible co-occurrences (Mueller-Dombois and Ellenberg 1974). The index is described by,

$$I_s = \frac{2c}{(a+b)}$$

where a is the number of species in area A, b is the number of species in area B, and c is the number of species in common to both areas A and B.

A randomized complete block design analysis of variance (RCB ANOVA) was used to compare species richness of the old-growth study sites with that of their secondary-growth matches (Mueller-Dumbois and Ellenberg 1974). Seven subsets of species richness were also tested to examine possible associations: tree species, total herbaceous species, woodland herbaceous and vernal herbaceous species, species reliant on wet soils, dry and/or disturbed soils, and moist and/or rich soils.

Species abundance distributions were compared for old- versus secondary-growth forest types, as well as by individual study site. These comparisons were viewed as a way of comparing the general establishment and vigor of species populations in the sites and between the two forest types. Differences in abundance class distributions of total, tree, herbaceous, woodland herbaceous, and vernal herbaceous populations were tested for significance using Chi-square test for independence.

RESULTS

One hundred forty-seven species in 55 families were encountered in the combined 45.7 ha of the six sites (Appendix A). Herbaceous species composed the majority of the flora at all sites (Figure 8). Within the herbaceous flora, 91.2% of the total list was classified as woodland species, 26.2% as vernal species, and 9.8% as nonwoodland species. Only one non-native species (*Taraxacum officinale*) was encountered. One hundred thirty-two species were found in the old-growth sites and 92 species were found in the secondary forest sites. Of those species occurring in the old-growth sites, 55 species (53.9% of the old-growth flora) were unique to only that forest type, while 17 species (27.9% of the secondary site flora) were unique to the secondary sites. Twenty-eight species (19% of the total flora) were common to all sites. In all cases, old-growth study sites were richer in species associated with wet soils and species associated with moist and/or rich soils (Figure 9). No clear trend was apparent for species associated with dry soils.

Numerical classification of the study sites using TWINSPAN and abundance data of all species present separated the secondary-growth sites from the old-growth sites in two divisions (Table 3; Figure 10). The first division separated the three secondary-growth sites and LB from the Bowl and SP sites. The second division removed LB from the secondary-growth grouping. Numerical classification of the study sites using abundance values of species associated with moist and/or rich soils separated the secondary-growth sites from the old-growth sites in three divisions. In the classification analyses using total herbaceous species, woodland herbaceous species and species associated with wet soils, TWINSPAN grouped the study sites in a somewhat similar

Figure 8. Total, herbaceous, tree, and shrub richness by study site. Old-growth sites were the Bowl, Shingle Pond and Lafayette Brook; secondary-growth sites were Bowl-match, Shingle Pond-match and HBEF W6.

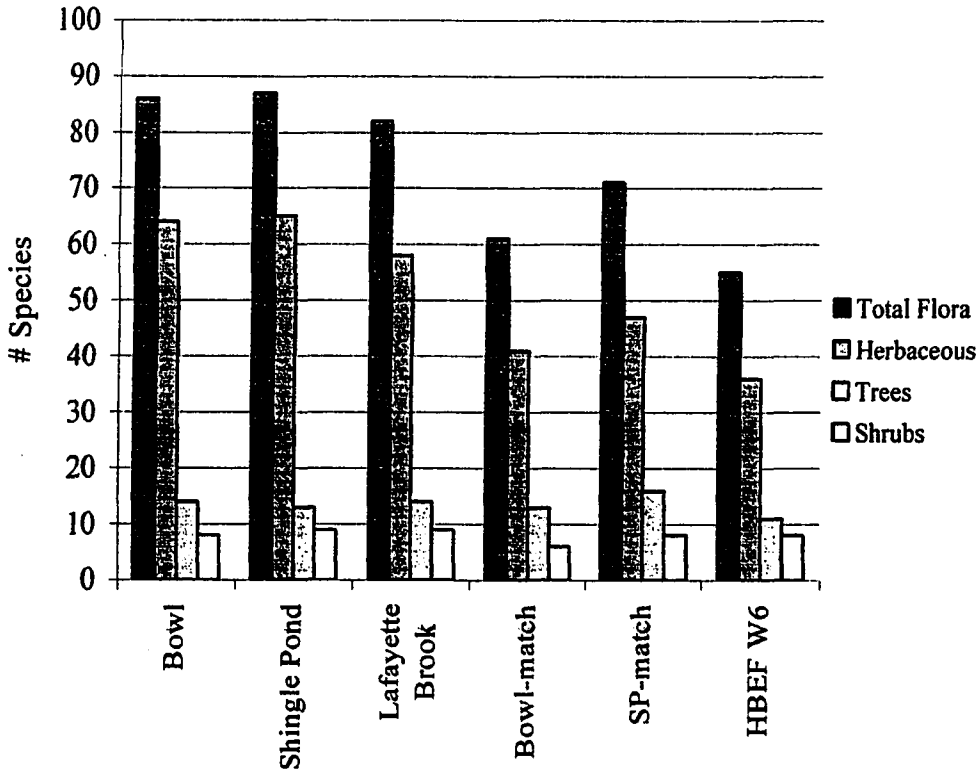


Figure 9. Species richness by study site of species associated with moist and/or rich soils, wet soils, and dry and/or disturbed soils. Old-growth sites were the Bowl, Shingle Pond and Lafayette Brook; secondary-growth sites were Bowl-match, Shingle Pond-match and HBEF W6.

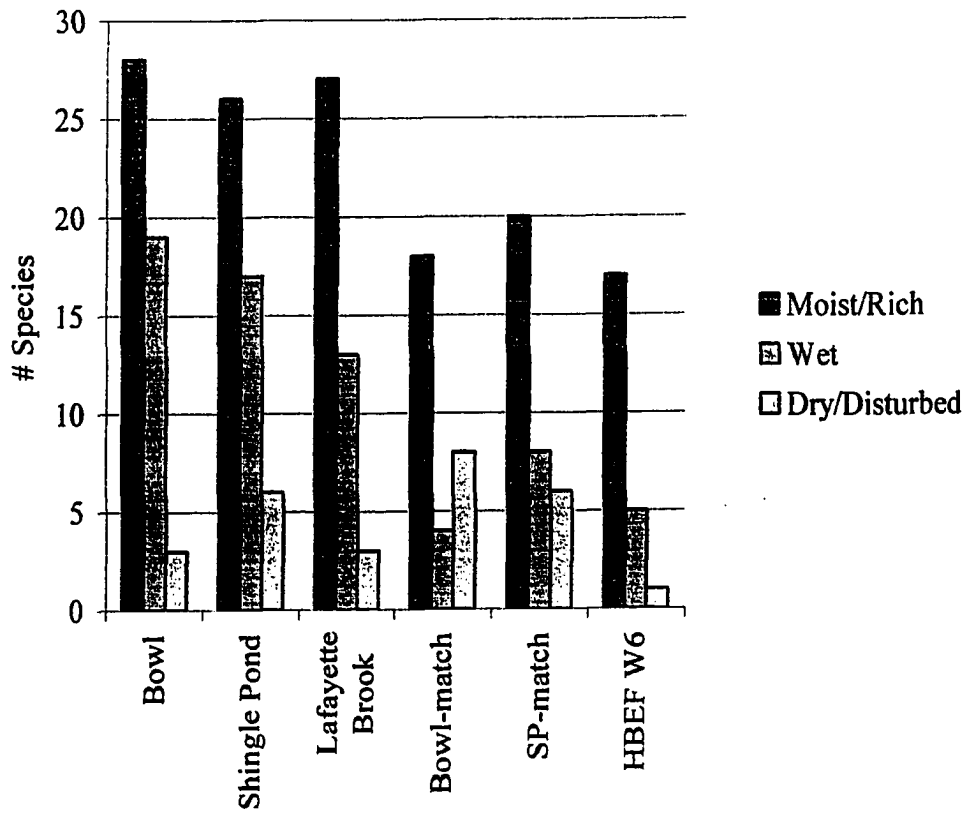


Table 3. Abbreviated species abundance matrix adapted from TWINSPAN two-way ordered table for the total flora, based on ranked abundance values of 147 species (see Appendix 2 for unabridged table). Order of the six samples (sites) is Lafayette Brook (LB), Bowl-match (B-m), Shingle Pond-match (SP-m), HBEF W6 (W6), The Bowl, Shingle Pond (SP). Results of the first two divisions are shown below. Old-growth sites were the Bowl, Shingle Pond and Lafayette Brook; secondary-growth sites were Bowl-match, Shingle Pond-match and HBEF W6.

	LB	B-m	SP-m	W6	Bowl	SP
Carex debilis	4	-	-	-	-	-
Tiarella cordifolia	5	-	-	-	-	-
Dryopteris carthusiana	-	-	3	2	-	-
Amelanchier laevis	-	4	4	-	-	-
Lycopodium clavatum	-	4	-	-	-	-
Pteridium aquilinum	-	4	4	-	-	-
Solidago rugosa ssp. *rugosa*	-	3	3	-	-	-
Claytonia caroliniana	4	-	-	-	2	-
Polystichum acrostichoides	3	-	-	-	2	-
Ribes lacustre	3	-	-	-	3	-
Carex deflexa	4	-	-	-	-	3
Carex scabrata	3	-	-	-	3	3
Dryopteris campyloptera	4	-	-	-	5	2

Thalictrum pubescens	2	-	-	-	4	-
Solidago macrophylla	2	-	-	-	3	4
Actaea pachypoda	-	-	-	-	3	4
Actaea rubra	-	-	-	-	-	5
Cardamine pensylvanica	-	-	-	-	3	2
Chelone glabra	-	-	-	-	4	3
Epilobium glandulosum	-	-	-	-	3	3
Eupatorium rugosum	-	-	-	-	5	-
Euthamia graminifolia	-	-	-	-	4	2
Galium triflorum	-	-	-	-	4	-
Glyceria melicaria	-	-	-	-	4	-
Impatiens capensis	-	-	-	-	4	-
Lycopus uniflorus	-	-	-	-	-	4

First division:	[LB	B-m	SP-m	W6]	[Bowl	SP]
	0	0	0	0	1	1

Second division:	LB	[B-m	SP-m	W6]
	0	1	1	1

Figure 10. Dendrograms of TWINSPAN classification of study sites, using species abundance values of a) the total flora and b) species associated with moist and/or rich soils conditions. Old-growth sites were the Bowl, Shingle Pond and Lafayette Brook; secondary-growth sites were Bowl-match, Shingle Pond-match and HBEF W6.

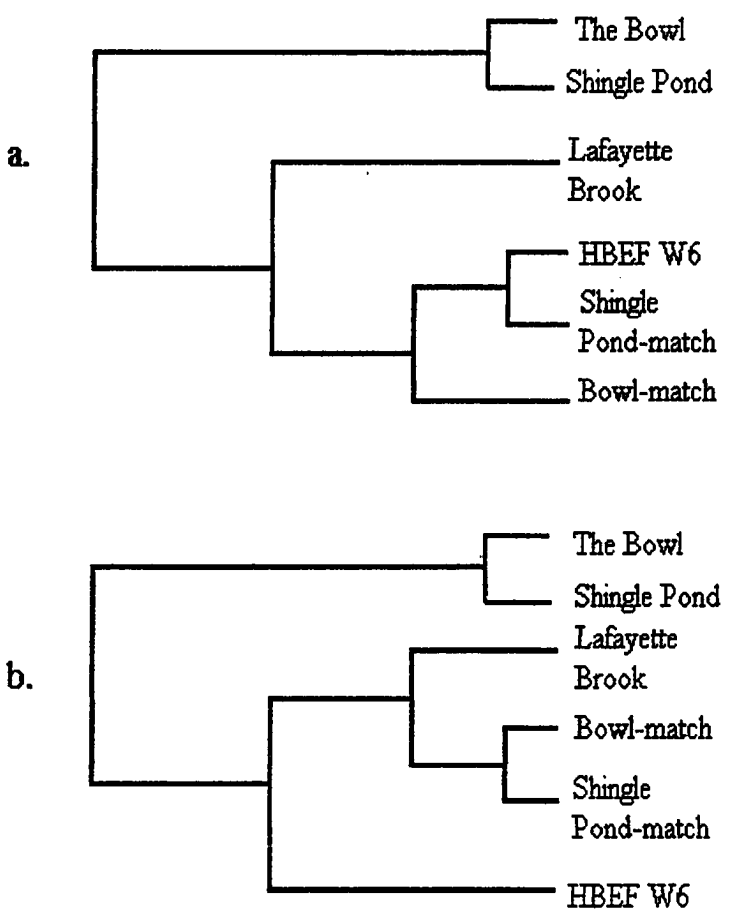
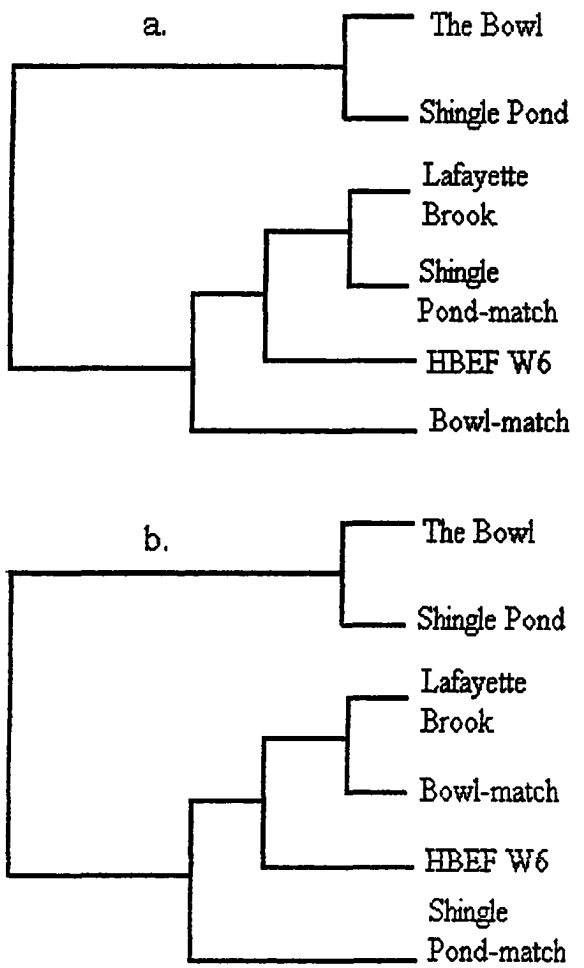


Figure 11. Dendrograms of TWINSPAN classification of study sites using species abundance values of a) the total herbaceous flora and b) the woodland herbaceous flora. Old-growth sites were the Bowl, Shingle Pond and Lafayette Brook; secondary-growth sites were Bowl-match, Shingle Pond-match and HBEF W6.



manner, the exception being in the placement of LB. In all three analyses, this old-growth site remained closely nested within the secondary-growth group (Figure 11). Numerical classification of vernal herbs, spring ephemeral herbs, species associated with wet soils and species associated with dry and/or disturbed soils yielded no discernable patterns with respect to the two forest types.

Tree species were identified by TWINSPAN as occurring in all old-growth sites, but in no secondary-growth sites (Table 4). Ten species occurred in two of three old-growth study sites but no secondary-growth sites and 42 species occurred only in one old-growth study site. There were no species which occurred in all three secondary-growth sites but no old-growth sites. However, four species occurred in two of three secondary-growth sites but no old-growth sites, and 13 species occurred only in one secondary-growth study site (Table 5). Herbaceous species accounted for 89.1% of the species unique to old-growth sites, but only 52.9% of the species unique to secondary-growth sites.

Mixed results were obtained clustering sites with Ward's minimum variance method, using the total flora. Three agglomerations were necessary to group the three secondary-growth sites and LB old-growth site remained nested within this cluster (Figure 12). Stronger results were seen, however, for Ward's clustering using the total herbaceous, woodland herbaceous and vernal herbaceous flora, and also using species associated with wet soils and species associated with moist and/or rich soils. In all five analyses, secondary-growth sites were grouped in two agglomerations (Figures 12 and 13). While the total herbaceous, woodland herbaceous and species associated with wet soils analyses were 100% chained (vernal herb and species associated with moist and/or

Table 4. The 55 herbaceous, shrub and tree species which were unique to old-growth (o-g) sites. Listed are the taxa that occured in one, two or all three old-growth sites. Species are indicated as associated with moist and/or rich soils*, wet soils*, or dry and/or disturbed soils[d] (Gleason and Cronquist 1991; Voss 1985, 1996).

	occurred in all o-g sites	occurred in 2 o-g sites	occurred in 1 o-g site	
Herbs	*Carex scabrata***	*Actaea pachypoda**	*Actaea rubra**	
	*Dryopteris campyloptera**	*Cardamine pennsylvanica***	*Anemone quinquifolia**	*Galium circaezans***
	*Solidago macrophylla**	*Carex deflexa***	*Aralia racemosa**	*Galium triflorum***
		*Chelone glabra***	*Arisaema triphyllum***	*Gaultheria hispidula*
		*Claytonia caroliniana**	*Aster lanceolatus**	*Glyceria melicaria***
		*Epilobium glandulosum***	*Aster macrophyllus*[d]	*Goodyera repens*
		*Euthamia graminifolia**	*Aster* sp. 1	*Impatiens capensis***
		Polystichum acrostichoides	*Aster* sp. 2	*Lycopus uniflorus***
		*Thalictrum pubescens***	*Botrichium simplex**	*Mitella nuda***
			Carex debilis	*Osmunda claytoniana**
			Carex leptonervia	Poaceae sp. 1
			Cerastium arvense[d]	Poaceae sp. 2
			Cirsium sp.	Poaceae sp. 3
			*Cornus canadensis**	*Pyrola rotundifolia*
			*Dicentra cucullaria**	*Scutellaria lateriflora***
			Dryopteris marginalis	*Solidago canadensis*
			*Epilobium ciliatum***	*Taraxacum officinale*[d]
			Erigeron strigosus[d]	*Tiarella cordifolia**
			*Eupatorium rugosum***	*Veratrum viride***
Shrubs		*Ribes lacustre***	*Rubus elegantulus*[d]	
			*Nemopanthus mucronatus***	
			Vaccinium angustifolium	
Trees			*Corylus americana*	
			*Tilia americana**	

Table 5. The 17 herbaceous, shrub and tree species which were unique to secondary-growth (2°) sites. Listed are species occurring in one, two or all three secondary-growth sites. Species are indicated as associated with moist and/or rich soils*, wet soils** or dry and/or disturbed soils[d] (Gleason and Cronquist 1991; Voss 1985, 1996).

	occurred in all 2° sites	occurred in two 2° sites	occurred in one 2° site
Herbs		*Dryopteris carthusiana*	*Botrychium oneidense**
	(none)	*Pteridium aquilinum*[d]	*Carex* sp. 1
		Solidago rugosa[d]	*Carex* sp. 2
			Epigea repens
			*Habenaria orbiculata**
			Lycopodium clavatum[d]
Shrubs		*Amelanchier laevis*[d]	*Ribes glandulosum***
			Spiraea tomentosa[d]
			*Viburnum nudum**
Trees			*Ostrya virginiana*
			Pinus resinosa[d]
			Populus grandidentata[d]
			Quercus rubra

Figure 12. Dendrogram produced by Ward's minimum variance clustering of the study sites using a) total, b.) herbaceous and c.) woodland herbaceous species abundance data. Distances are Euclidean.

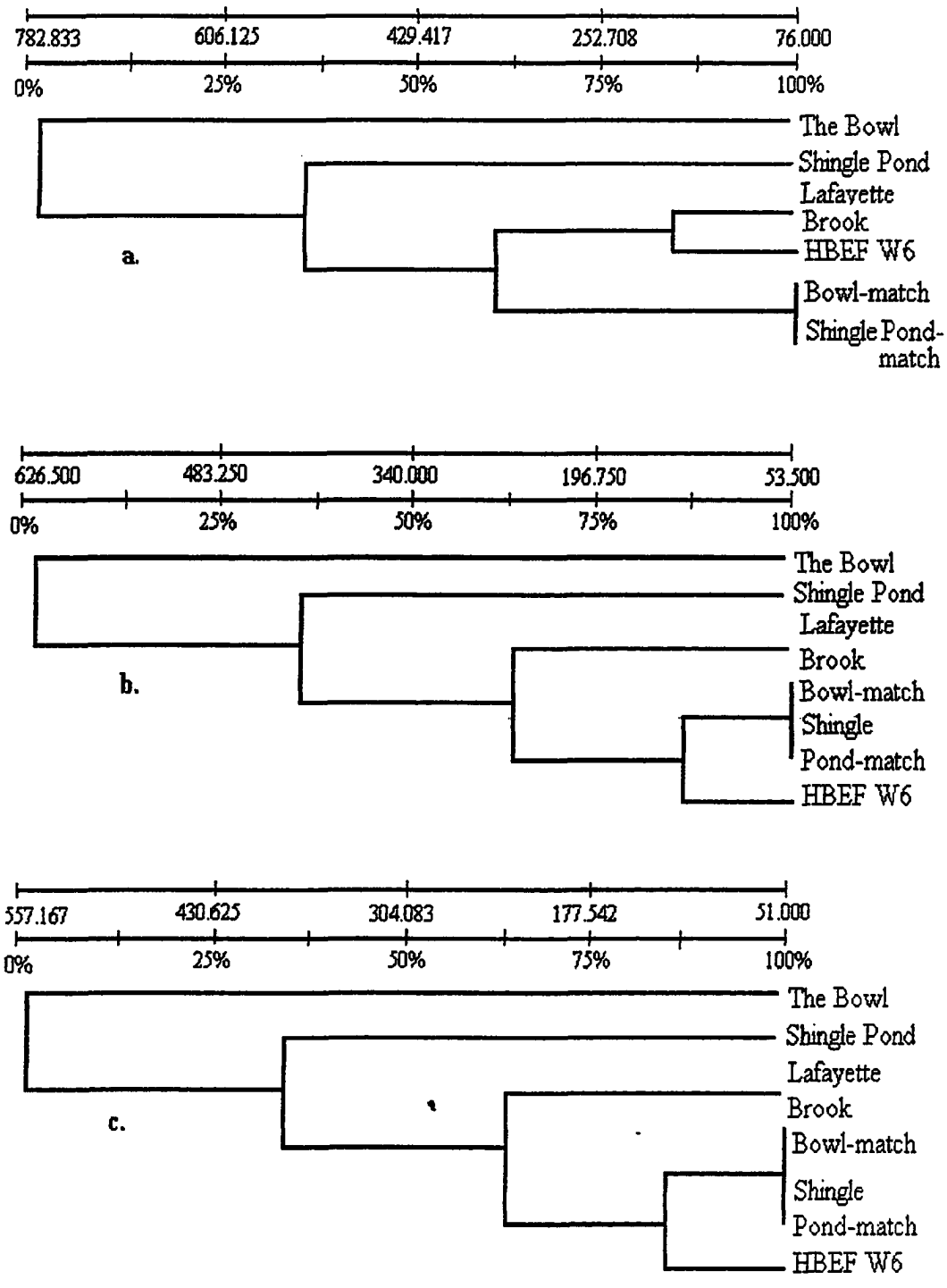
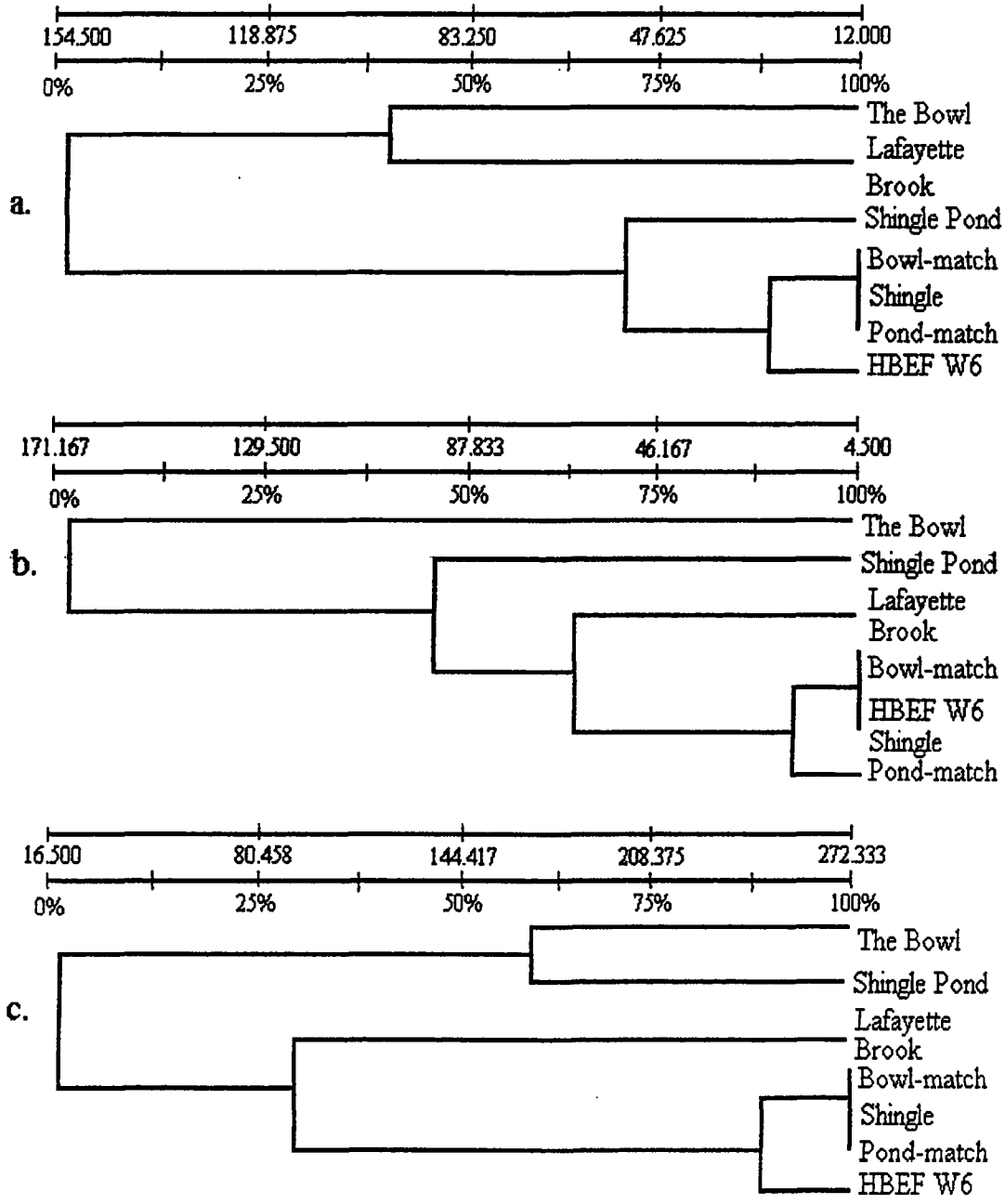


Figure 13. Dendrograms produced by Ward's minimum variance clustering of the study sites using abundance data of a) vernal herbaceous species, b) species associated with wet soils and c) species associated with moist and/or rich soils. Distances are Euclidean. Old-growth sites were the Bowl, Shingle Pond and Lafayette Brook; secondary-growth sites were Bowl-match, Shingle Pond-match and HBEF W6.



rich soils datasets chained 25%), this was interpreted as appropriately revealing a true floristic relationship amongst the study sites (Pielou 1984) which were, after all, chosen for their biotic and abiotic similarities. The sites did not cluster using spring ephemeral herbaceous data.

Similarity of the total flora ranged from 61.2% to 85.7% between the sites, according to Sørensen's Index, with the Bowl and its match, B-m, exhibiting the lowest similarity in floristic composition, and Bowl and the LB exhibiting the highest similarity (Table 6). Old-growth sites were more floristically similar to one another, but exhibited more within-group variation than did the secondary sites ($\bar{X}_{OG} = 0.731$, $s = 0.110$; $\bar{X}_{2^\circ} = 0.691$, $s = 0.0763$). The old-growth and secondary forest environmentally-matched pairs (Bowl and B-m, SP and PS-m, LB and W6) showed the lowest mean floristic similarity, as well as the least group variation ($\bar{X}_{MP} = 0.643$, $s = 0.0297$; Figure 14). Sørensen's Index for the herbaceous flora showed similar trends, with the old-growth floras exhibiting even greater mean similarity than the secondary group, but with greater standard deviation ($\bar{X}_{OG} = 0.732$, $s = 0.183$; $\bar{X}_{2^\circ} = 0.688$, $s = 0.0932$; $\bar{X}_{MP} = 0.602$, $s = 0.0497$; Table 6). The tree community showed the greatest degree of similarity overall, with the old-growth group still ranking most similar ($\bar{X}_{OG} = 0.878$, $s = 0.0578$; $\bar{X}_{2^\circ} = 0.725$, $s = 0.0578$; $\bar{X}_{MP} = 0.778$, $s = 0.0578$). None of these mean differences were significant according to two-sample t-tests for the means.

Patterns differed for the vernal herbaceous flora, with Sørensen's Index revealing SP and SP-m as the most similar and SP and LB as the least similar. This matrix was generated to explore SP's notably depauperate vernal flora, relative to the other old-growth sites. The group mean of SP's similarity to secondary-growth sites was higher than either the Bowl or LB's group means to these sites ($\bar{X}_{SP/2^\circ} = 0.815$, $s = 0.0578$; $\bar{X}_{Bowl/2^\circ} = 0.770$, $s = 0.0468$; $\bar{X}_{LB/2^\circ} = 0.729$,

Table 6. Sørensen's Index of Similarity matrices for a.) total flora, b.) herbaceous flora, c.) vernal herbaceous flora. Main diagonal (bold) is the number of species in each site, above the main diagonal is Sørensen's index, below the main diagonal is the number of species in common to both sites. Old-growth sites were the Bowl, Shingle Pond (SP) and Lafayette Brook (LB); secondary-growth sites were Bowl-match(B-m), Shingle Pond-match (SP-m) and HBEF W6 (W6).

a.

	Bowl	SP	LB	B-m	SP-m	W6
Bowl	**87**	0.686	0.857	0.612	0.637	0.643
SP	59	**87**	0.651	0.635	0.671	0.634
LB	78	54	**81**	0.704	0.697	0.647
B-m	45	47	50	**60**	0.779	0.655
SP-m	50	53	53	51	**71**	0.640
W6	45	45	44	38	40	**55**

b.

	Bowl	SP	LB	B-m	SP-m	W6
Bowl	**65**	0.641	0.943	0.547	0.595	0.586
SP	41	**65**	0.612	0.598	0.643	0.580
LB	58	37	**58**	0.660	0.686	0.617
B-m	29	32	33	**41**	0.795	0.641
SP-m	33	36	36	35	**47**	0.627
W6	29	29	29	25	26	**36**

c.

	Bowl	SP	LB	B-m	SP-m	W6
Bowl	**20**	0.765	0.732	0.743	0.824	0.743
SP	13	**14**	0.686	0.759	0.857	0.828
LB	15	12	**21**	0.722	0.743	0.722
B-m	13	11	13	**15**	0.828	0.733
SP-m	14	12	13	12	**14**	0.759
W6	13	12	13	11	11	**15**

$s = 0.0121$). It was also higher than either old-growth or secondary-growth within-group means ($\overline{x}_{OG} = 0.728$, $s = 0.0397$; $\overline{x}_{2^o} = 0.773$, $s = 0.0491$), though none of these mean differences were significant according to two-sample t-tests for the means.

Results for RCB ANOVA analyses revealed significantly greater total species richness ($F_{1,2} = 51.857$, $p = 0.0187$), herbaceous species richness ($F_{1,2} = 240.25$, $p = 0.004$), and unique herbaceous species richness ($F_{1,4} = 33.8$, $p = 0.00436$) in the old-growth sites as compared to secondary-growth sites. Old-growth sites were also richer than secondary sites in shrub species ($F_{1,2} = 16.000$, $p = 0.057$; Figure 15), species reliant on wet soils ($F_{1,2} = 12.488$, $p = 0.024$), and species associated with moist and/or rich soils ($F_{1,2} = 6.761$, $p = 0.060$), though not significantly so. It should be noted that, while not significant according to this study's $P = 0.025$ standard, ANOVA results for the wet species list closely approached significance. No clear pattern was seen for species associated with dry soils and ANOVA results were not significant ($F_{1,4} = 0.0938$, $p = 0.775$). Secondary-growth sites were richer than old-growth sites in tree species, though not significantly so ($F_{1,2} = 0.429$, $p = 0.868$). Within the herbaceous flora, the number of uniquely occurring herbaceous species and woodland herbaceous species were significantly greater in the old-growth sites ($F_{1,4} = 33.800$, $p = 0.00436$, and $F_{1,2} = 81.757$, $p = 0.012$, respectively). Vernal and spring ephemeral herbs, while again richer in old-growth sites, were not found to be significantly so ($F_{1,2} = 3.903$, $p = 0.187$, and $F_{1,4} = 0.893$, $p = 0.398$, respectively).

In all cases, the model using untransformed data provided the best fit for the analyses, showed no trends in the residuals, and was chosen as the working model. Due to the low numbers of unique and spring ephemeral species in the secondary-growth sites, and the low numbers of species associated with dry soils in the old-growth sites, the blocking

Figure 14. Sørensen's Index of Similarity within-group a.) means and b.) standard deviations for old-growth, secondary-growth and matched-pairs study sites. Tree, shrub, herbaceous and total flora results are presented.

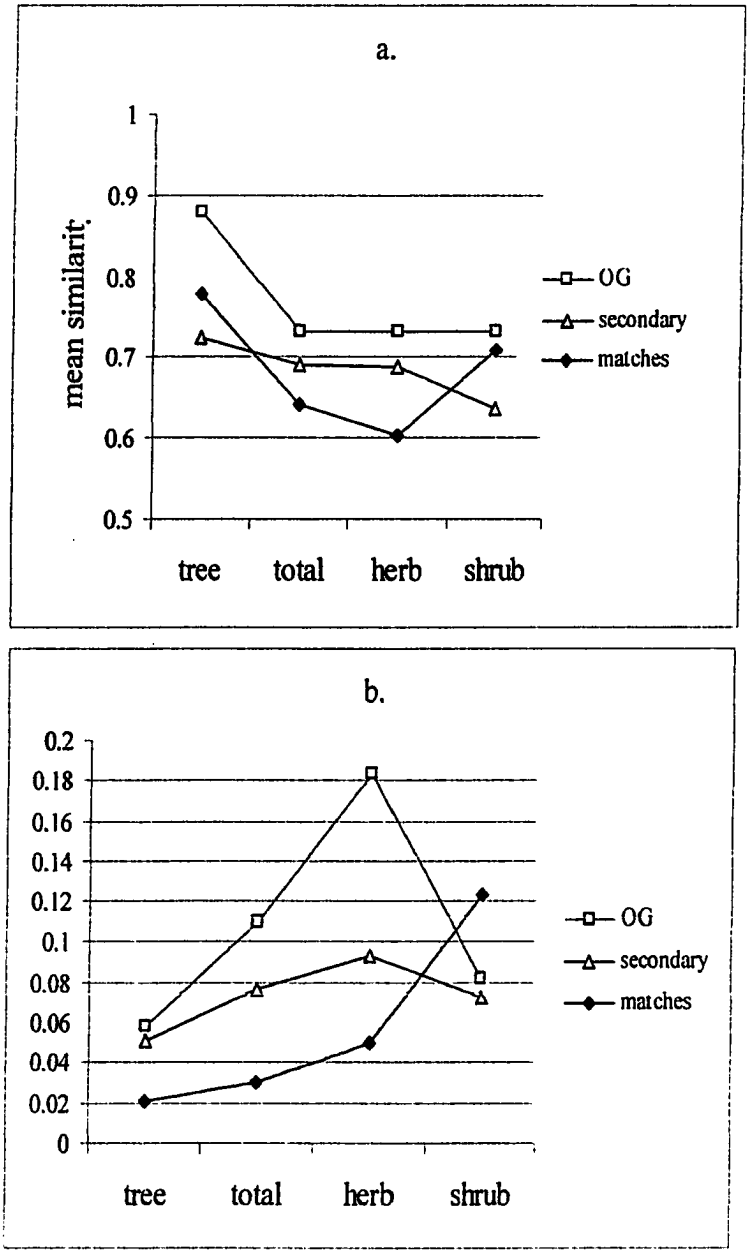
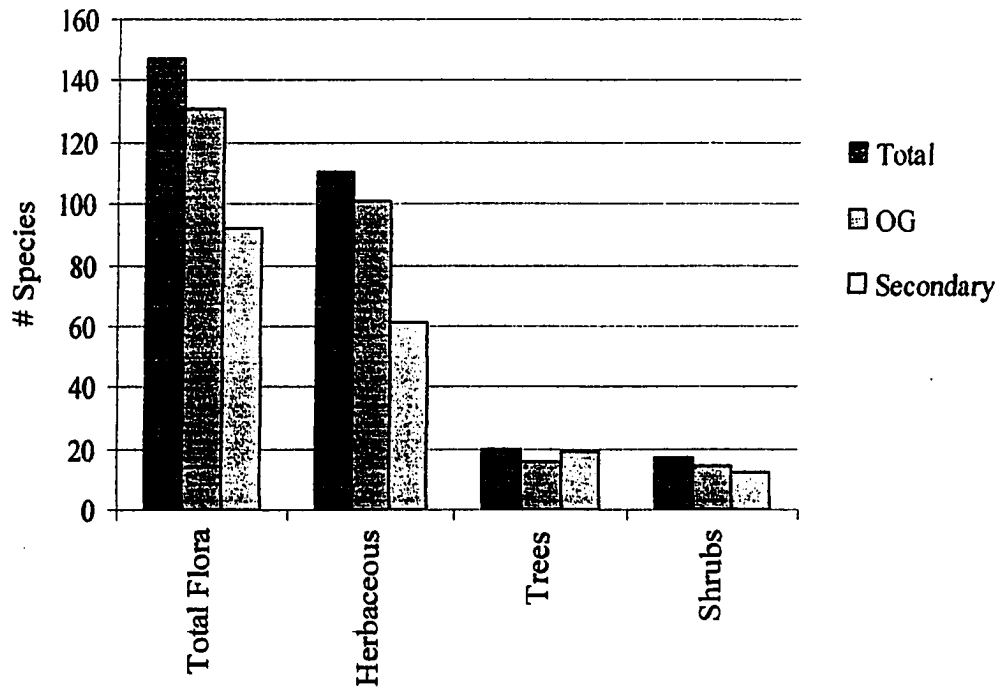


Figure 15. Total, herbaceous, tree and shrub species richness by old-growth and secondary-growth study sites.

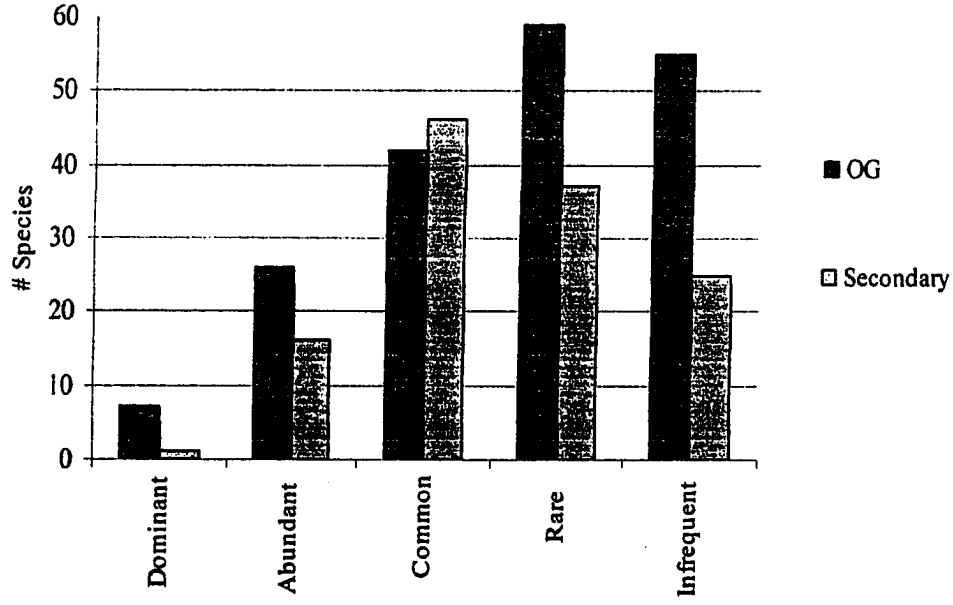


factor was removed from those analyses.

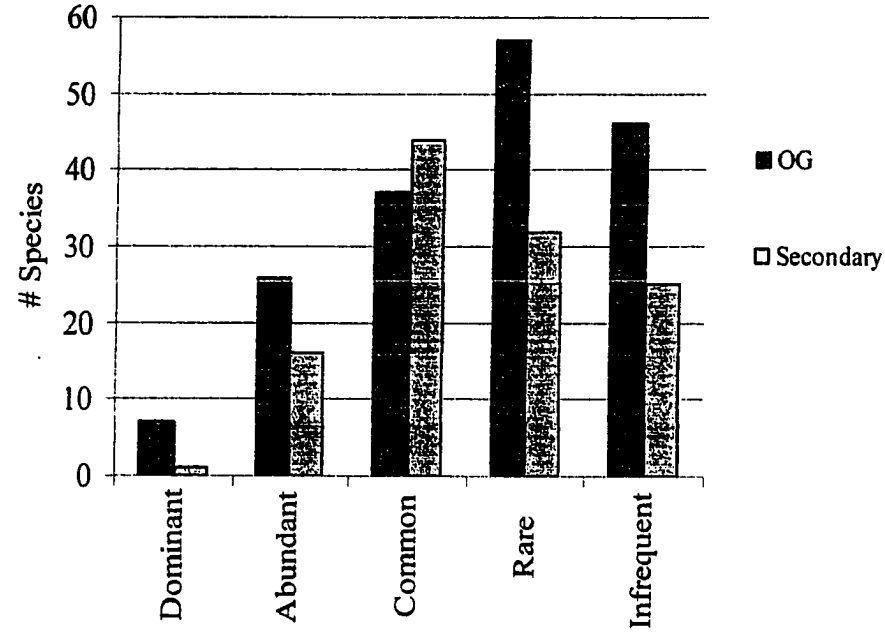
Total herbaceous and woodland herbaceous species abundance distributions were found to be significantly different in old-growth versus secondary-growth sites, according to Chi-square tests for independence, $P < 0.05$ (herbaceous: $X^2 = 10.757$, $p = 0.0294$; woodland herbaceous: $X^2 = 10.707$, $p = 0.0301$). Subjective examination of the graphed data revealed that old-growth species distributions were skewed to the right, relative to secondary-growth distributions, indicating a greater frequency of occurrence of species with "infrequent" or "rare" abundance values in old-growth sites (Figure 16). More species with "dominant" abundance values also occurred in old-growth sites. While different distributional patterns were also revealed between the two forest types for total, tree, shrub, vernal herbaceous, and spring ephemeral species, these differences were not significant (for df = 4, total flora: $X^2 = 7.837$, $p = 0.0977$; tree: $X^2 = 1.034$, $p = 0.905$; shrub: $X^2 = 1.302$, $p = 0.861$; vernal herbaceous: $X^2 = 6.744$, $p = 0.150$; spring ephemerals: $X^2 = 1.373$, $p = 0.849$).

Figure 16. Species abundance distributions for a) total herbaceous flora and b) woodland herbaceous flora in old-growth and secondary-growth sites.

a.



b.



DISCUSSION

The results of this study concur with those of the few other comparative studies of eastern deciduous forests in finding significant differences between old-growth and mid-successional secondary forests floras. Classification of the six study sites by total floras using TWINSPAN separated secondary from old-growth floras in 2 divisions, results which were corroborated by cluster analysis. Cluster analysis also grouped secondary-growth sites using total herbaceous, woodland herbaceous and vernal herbaceous species abundance data. Old-growth floras were significantly richer in herbaceous species, specifically woodland herbaceous species, and these species showed significantly different abundance distributions relative to secondary floras. Old-growth floras included more species of small population size and were significantly richer in unique herbaceous species. Differences in the number of species associated with wet soils closely approached statistical significance. Sørensen's similarity index indicated old-growth floras to be more similar in their tree, shrub and herbaceous communities than secondary floras.

Sorensen's index showed old-growth sites the Bowl and LB to have the greatest similarity of both total and herbaceous floras, yet TWINSPAN and cluster analyses suggested the Bowl's flora to be more similar to Shingle Pond's, often nesting Lafayette Brook within secondary site groupings. While species richness and abundance was used in both site classification analyses, Sørensen's index compared study sites using only species richness. Differences between the results of the classification analyses and Sørensen's may therefore be due to differences in species abundance of many or even a few species. It should also be noted that the 3rd and 4th most similar sites in Sørensen's total and total herbaceous analyses were LB

and secondary-growth sites B-m and SP-m, respectively (secondary-growth sites B-m and SP-m ranked 2nd). Such close associations may also help to explain the nesting of LB in secondary-growth clusters.

These results can be interpreted by various theoretical models of species diversity, but are comprehensively explained by the *general model of diversity* suggested by Petraitis et al. (1989). This model attempts to explain why most equilibrium and nonequilibrium hypotheses alike predict maximum species diversity at intermediate levels of disturbance or predation (Petraitis et al. 1989). Perhaps the best known model of species diversity and disturbance is Connell's *intermediate-disturbance hypothesis* (1978), in which disturbance prevents the system from reaching equilibrium, thus suppressing the rate of competitive exclusion and maximizing the number of species able to coexist. Petraitis et al. (1989) demonstrated that the definition of whether a system as at equilibrium or not is merely a matter of scale and believed it probable that theories pertaining to these two states may converge when disturbance is small and frequent enough to act like predation. Their general model combines Huston's (1979) *dynamic-equilibrium model* and MacArthur and Wilson's (1963) *island biogeography theory* in predicting species diversity as a function of disturbance, productivity, competitive exclusion, life-history characteristics, and rates of immigration and extinction within the system. Grime (1979) and MacArthur and Wilson (1963) showed that life-history characteristics limit species from being highly tolerant of both disturbance and competition. At intermediate levels of disturbance trade-offs in species-specific abilities regulate birth and death rates, as well as rates of immigration and extinction, maximizing the number of disturbance-tolerant and competition-tolerant species able to coexist.

The *general model of diversity* (Petraitis et al. 1989) predicts maximum diversity at low to intermediate disturbance levels in systems characterized by low species growth rates, low rates of competitive exclusion and extinction, and intermediate rates of immigration. Although not directly measured by this study, it is theorized that the high level of species richness in old-growth floras is directly or indirectly the result of canopy gap dynamics coupled with the life-history characteristics of late-successional species, which together foster all these conditions. Gap dynamics in old-growth systems can be theoretically shown to constitute an intermediate level of disturbance at the stand level, creating conditions of lowered rates of extinction and competitive exclusion, and higher rates of immigration as compared to secondary systems. By comparison, the mid-successional secondary forests studied here will be argued to be systems with relatively low rates of disturbance and relatively high recent rates of competitive exclusion and extinction. Intensive tree harvesting and the resultant conversion of these systems to earlier successional conditions have resulted in the disruption of gap dynamics and a reduction in habitat heterogeneity at the stand level. Changed conditions in secondary sites as a result of harvesting may have also contributed to the floristic differences identified in this study. Rates of immigration to mid-successional secondary-growth forests are low as life-history traits of late-successional species make them inefficient dispersers and colonizers of new areas. Such conditions have resulted in a perhaps prolonged period of understory repression and lowered species richness in these forests.

I. Gap dynamics in eastern old-growth forests

a. Background

The importance of gap-phase dynamics to old-growth forests has been much discussed in the literature. Bormann and Likens (1979) reported that the natural cycle of catastrophic disturbance events in beech-maple old-growth forests probably approaches or exceeds 1000 years, over three times the average lifespan of the system's dominant individuals (Davis 1996, Runkle 1991). Most natural disturbance to these systems is therefore small in scale, by way of individual tree deaths or the death of small groups of trees. Age distributions of canopy trees in old-growth forests indicate that tree species are self-replacing in a "patchy" manner, leading researchers to refer to old-growth gap forests as shifting mosaics of patches of forest at different successional ages (Bormann and Likens 1979; Connell 1989; Petraitis et al. 1989; Runkle 1991).

Most canopy tree deaths in New England forests are caused by wind stress and/or predation from fungi, insects or disease (Kimball et al. 1995; Tyrrell and Crow 1994; Worrall and Harrington 1988). It's estimated that 1% of the old-growth canopy is opened by new treefalls annually (Clebsch and Busing 1989; Moore and Vankat 1986; Runkle 1991). Runkle (1982) found that gaps of various ages occupied anywhere from 3.2-24.2% of the canopy of old-growth hardwood stands he studied, and Lorimer (1989) estimated an average of 70% of old-growth canopies to be occupied by large, mature tree crowns at any given time. Size of these gaps is important to species composition, as small gaps are quickly closed by lateral crown expansion and favor shade-tolerant species, whereas large gaps close only with tree replacement over many years, thus favoring shade-intolerant species (Clebsch and Busing 1989). Lorimer's (1989) review of the literature classified

average gap size in temperate old-growth forests to be 280 m^2 to 375 m^2 in size (also see Clebsch and Busing 1989), although Tyrrell and Crow (1994) found average gap size in 25 old-growth hardwood-hemlock stands in Wisconsin and Michigan to be > 50 m^2, with 30% < 10 m^2 and few gaps > 250 m^2.

b. Gaps and environmental heterogeneity

The effects of gap-phase dynamics include openings in the canopy, "pit and mound" microtopography and an increase in the system's volume of leaf litter and coarse woody debris (CWD) in all stages of decay. Gap-phase dynamics increase both the number of resource conditions and the number of physical microhabitats in old-growth forests. This increase in environmental heterogeneity should theoretically foster high species diversity (see Whittaker et al.1974). Treefalls create depressions and hummocks on the forest floor (pits and mound topography), exposing small areas of mineral soil with differing nutrient availability, cation-exchange capacity and pH (Beatty 1984), and creating catchments for precipitation and decaying organic matter (Bratton 1976; Moore and Vankat 1986). Openings in the canopy increase light, air temperatures, soil moisture, and soil temperature within the microenvironment of the patch (Moore and Vankat 1986; Schultz and Adams 1995; Walters and Stiles 1996). Leaf litter and decaying wood provide low nutrient, high moisture environments that are important germination sites for several plant species (Meier et al. 1995; Moore and Vankat 1986; Runkle 1991). This gradient of resource conditions created by canopy openings increases heterogeneity of the forest floor and results in greater availability of coarse woody debris (CWD) in various stages of decay. Both have been theorized by Goebel et al. (1999) and Meier at al. (1995)

to be responsible for the higher species diversity in old-growth sites. Bratton (1976) believed only seasonal changes in light competed with the importance of microtopography in influencing herbaceous species distributions in Appalachian cove ecosystems.

c. Species diversity and gap size

Size and orientation are both important determinants of species composition within canopy gaps (Schultz and Adams 1995). Diversity studies of different sized gaps are not plentiful, but most references in the literature maintain that only large gaps increase species richness at the stand level (Collins and Pickett 1988; Lorimer 1989). Moore and Vankat (1986) reported greater abundance but no significant differences in herbaceous species richness in the small (i.e., single treefall) gaps they studied in the old-growth beech-maple forests of Hueston Woods, Ohio. Kimball et al. (1995) compared small gaps (< 50 m^2) in young secondary forests with large harvest-created gaps (averaging 225 m^2) and found the latter promoted significantly richer herbaceous species compositions. Lorimer (1989) suggested managing for diversity with gaps ≥ 500 m^2, although further research is being conducted regarding such estimates (Margolis 2002).

Clebsch and Busing (1989) reported that a wide range of gap sizes in forests accommodates a larger variety of species, including more shade-intolerants. Large gaps offer greater opportunity for new species immigrations, specifically with respect to wind-dispersed ruderals. The case of the Shingle Pond old-growth site in this study illustrated this point. Shingle Pond contained the largest number of nonwoodland herbaceous species of any site (6, as compared to none for HBEF Watershed 6 and 2 for all other

sites), four of which were wind-blown ruderals (*Cirsium* sp., *Erigeron strigosus, Euthamia graminifolia, Taraxacum officinal).* The likeliest explanation for this is that this site was also observed to have the largest percent of open canopy, probably due to damage during an unusually severe ice storm in 1998. Damage from such storms results from ice coating tree limbs heavily enough to break portions of the canopy. The ice storm of 1998 resulted in significant canopy damage at mid elevations throughout the WMNF (Rhoads et al. 2002).

It is possible that, while not explicitly observed, even smaller gaps contribute to the greater species diversity of old-growth forests. A shifting mosaic of gaps of various sizes and ages may allow these systems to maintain species which would otherwise be extirpated by offering revolving opportunities for reproduction and enrichment of the seed bank. There is good evidence that some understory species may require gap conditions for successful reproduction. Moore and Vankat (1986) and Menges (1986) observed that species common to their study areas frequently occurred in greater abundance in gaps, and that individuals in gaps appeared more robust and vigorous.

Moore and Vankat (1986) noted that woodland species produced more flowers in gaps, leading them to theorize that moisture and temperature differences in these microenvironments influenced vegetative and reproductive phenology patterns, assimilation rates, and resource allocation patterns. Walters and Stiles (1996) studied the reproductive phenology of *Impatiens capensis* in old-growth oak-hickory-beech stands in New Jersey and found pollinator visitation rates, floral densities and seed production all significantly higher in gaps (visitations increased, but not significantly, with the number of open flowers). They cite the sensitivity of pollinators to temperature, visibility, and the

quality of pollen/nectar rewards when foraging. The seeds of some shade-tolerant woodland species have been found to germinate significantly better in the higher light, heat and moisture conditions gaps provide (Anderson and Loucks 1973).

d. Gaps as an intermediate level of disturbance

If we look at the herbaceous dynamics of old-growth forests at the stand level then, their pattern can be represented as a mosaic of discreet species compositions experiencing a gradient of disturbance intensities. While most of the forest floor is under mature, intact canopy and experiencing little to no disturbance, over 20% may be experiencing intermediate to intense disturbance (small vs. large gaps). While most of the forest is at relative equilibrium with respect to species composition, some proportion is in the midst of active directional changes, a balance which has been referred to as "dynamic gap-phase equilibrium" (Bormann and Likens 1979). Such forests likely constitute an intermediate level of disturbance, and may possess a gradient of resource conditions within which a maximized number of species can coexist.

II. Conditions in mid-successional secondary-growth forests

a. Loss of gap-phase dynamics

While there are few published studies quantitatively comparing the effects of canopy gaps on herbaceous species diversity in eastern temperate old-growth versus mid-successional secondary-growth forests, most studies indicate that gap dynamics in these two systems differ significantly. Clebsch and Busing (1989) reported significant differences in the canopies of Appalachian cove forests, citing that old-growth forests

tended to have larger average gap size as well as gaps which were slower to close, resulting in a larger distribution of gap age classes across the stand. Older forests have been noted to have a higher rate of gap formation per year than mid-successional secondary forests and a more even distribution of all size classes (Runkle 1982; Tyrrell and Crow 1994). Lorimer's (1989) review of the literature concluded that treefalls in 60-80 year old secondary forests either did not create gaps or created gaps small enough that they were quickly closed by lateral crown expansion.

Most of the differences between old-growth and mid-successional forests have been attributed to differences in average tree age. Larger trees in old-growth forests have broader, overlapping crowns, whereas secondary canopies are composed of smaller crowns with little overlap (Clebsch and Busing 1989). Age estimates at which gap-phase dynamics typified by eastern old-growth forests will be reestablished in secondary forests vary: Duffy and Meier (1982) suggested that gaps may continue to decline in Appalachian forest systems for up to 87 years after being cut. Meier et al. 1995 believed that gap-phase processes may take 150-200 years to fully recover. Tyrrell and Crow (1994) found that both average gap size and percent of the canopy occupied by gaps increased linearly with stand age, suggesting recovery times might be estimated based on average lifespans of dominant trees.

There is clearly concern expressed in the literature that many late-successional species will suffer extirpation in secondary forests by the time gap-phase processes fully recover (Goebel et al. 1999; Halpern and Spies 1995; Meier et al.1995; Roberts and Zhu 2002; Spies 1991). The relationship between habitat diversity and species richness is well-documented, as is the decrease in habitat diversity resulting from the loss of gap-

phase dynamics. Besides the loss of median heat and light conditions, the forest floor environment of aggrading forests has been found to be more homogenous than that of older stands specifically because of the rarity of treefalls (Bormann and Likens 1979; Crozier and Boerner 1984).

Thompson (1980) and Rogers (1982) found herbaceous species that preferred treefall areas. Beatty (1984) reported that mounds and pits of old-growth hardwood forests had characteristically different assemblages of herbaceous species as compared to undisturbed ground, theorizing differences in resource availability and competitive dynamics as reasons for these specializations. Goebel et al. (1999) theorized that the exposure of mineral-rich soil in tip-up mounds accommodated species not found in their secondary sites. Tyrrell and Crow (1994) studied stand age structural development of 25 Wisconsin and Michigan hemlock-hardwood old-growth stands and reported that although total volume of CWD ("coarse woody debris"; logs in all decay classes) increased linearly over time, well-decayed logs occurred only after threshold age of 275-300 yrs. While they found area and density of tip-up mounds not correlated to stand age, they explained this as probably due to the persistence of these topographic features over long periods of time. Beatty (1984) believed treefall pits and mounds could potentially last several centuries if undisturbed.

Lacking the gap-phase dynamics which characterize old-growth systems, the 80-100 year old secondary-growth forests of this study and others are likely experiencing a relatively low rate of disturbance which has contributed to their lower species richness. This rate is likely to increase slowly over time, as canopy trees mature, until the gap-phase dynamics characteristic of old-growth systems are restored and species richness is

again maximized by intermediate disturbance conditions. Theoretically, this may take as long as the average lifespan of dominant tree species, which in the case of beech-maple forests of the northeast is approximately 300 years.

b. Soil changes as the result of harvesting

Long-term changes to the soil as the result of tree harvesting may also have detrimental effects on regenerating floras. Concern over the lasting effect of soil compaction, erosion, hydrological changes, and depletion of the seed bank has been cited in the literature (Bormann et al. 1974; Bormann and Likens 1979; Mou et al. 1993; Pierce et al. 1993). It remains unclear whether altered conditions in secondary stands, such as soil impoverishment and loss of soil moisture, may further diminish the suitability of these sites for colonization. Several studies have noted that soils of secondary-growth sites appeared drier and that species composition reflected this condition (Anderson and Loucks 1973; Moore and Vankat 1986), and Goebel et al. (1999) found differences in ground flora composition of old-growth versus 70-79 year old secondary forests correlated with differences in pH and depth of the A horizon.

While not directly measured, Teeling-Adams noted that both the secondary sites of this study, as well as those she surveyed within the Hubbard Brook Experimental Forest, appeared to have less interruption of waterways by downed logs and microtopographic features than was observed in old-growth sites. Such interruptions often resulted in more vernal streams, small stifles and wet seeps which clearly exhibited a greater diversity of herbaceous species than drier areas within the site. By contrast, streams in secondary sites were observed to be more direct and often of a perennial

nature. From these observations it can be theorized that, whether using conventional machinery or horse teams, a possible "grading" or homogenizing of the forest floor occurs in some secondary sites as a result of clearing large, felled trees from the land. Coupled with the effects of erosion and the suppression of new microtopographic features (the loss of pit and mound formation) this smoothing of microtopography may cause potentially significant changes in site drainage, such that a few major waterways remain where there once were countless secondary features. While the volume of water moving through an old-growth site and its secondary incarnation may be the same, this moisture may be distributed in very different ways. More research is needed in this area.

III. Life-history traits of "late-successional species"

Disturbance-tolerance, resource utilization and competitive dynamics in herbaceous species are closely tied to physiology and morphology (Bratton 1976; Grime 1973). MacArthur and Wilson (1963) classified species as r- or K-selected based on patterns of resource allocation (also see Gadgil and Solbrig 1972). K-selected species employ a strategy of restrained investment in growth and reproduction, and increased allocation to photosynthate storage in order to tolerate resource-poor conditions. Grime (1979) characterized species as ruderals, competitors or stress-tolerators according to life-history characteristics. Long lifespans with low seed production and low maximum potential growth rates characterize species of stressful systems with low productivity (Grime and Hunt 1975; MacArthur and Wilson 1963). Old-growth ecosystems have been well-documented to be stable, relatively unproductive environments and both models recognize that species adapted to such environments are limited in their ability to tolerate

disturbance (Bormann et al. 1974; Davis 1996; Whittaker et al. 1974).

a. Slow growth rates

Evidence for slow rates of growth in woodland species of the northeast is largely observational, but some empirical data do exist. Sobey and Barkhouse (1977) recorded the growth rates of 43 woodland herbaceous species in eastern Canada and found rates ranging up to 100 cm/year. Late-successional herbaceous taxa were the slowest growing, with many growth rates reported as undetectable. Whitford (1949) reported growth rates of late-successional woodland species in Illinois as 0.66-3.5 cm/year. Curtis (1943) studied five *Cypripedium* spp. and found *C. acaule* took 8-10 years to reach reproductive maturity, while *C. reginae* took 14-16 years. Moore and Vankat (1986) suggested the use of more stored materials for growth and reproduction may make late-successional species slower to respond to changing resource conditions, reducing competitive abilities in the event of disturbance. Rogers (1982) found long-lived perennial herbaceous species with large storage organs to be uncommon in the disturbed mesophytic forest sites he studied in the Great Lakes region.

b. Asexual reproduction and low seed production

Because of the tendency to allocate more energy to growth and storage, many late-successional species are functionally clonal (Beatty 1984; Whitford 1949). Asexual reproduction is energy efficient and an important strategy in environments where light and resources may be limiting. Beatty (1984) found vegetative reproduction the most common mode of herbaceous dispersal in the New York hardwood forests she studied.

Anderson and Loucks (1973) reported that *Trientalis borealis* apportioned 64.8% total dry weight to vegetative reproduction and storage (rhizomes and tubers) and < 2% to seeds. Whitney and Foster (1988) theorized that low seed production explained differences between primary and secondary understories in the Pisgah forests of Massachusetts and southern New Hampshire. The tendency toward clonal reproduction has long been considered a contributing factor in the slow migration rates of many woodland species (Beatty 1984; Whitford 1949). While Matlack (1994) found no significant difference between migration rates of clonal and exclusively sexual species, this may have been due to the extremely low rates of species of both types.

c. Inefficient dispersal mechanisms and migration

While the processes are not well yet understood, studies have suggested that inefficient dispersal mechanisms may be more significant than low reproduction rates in explaining low migration rates of late-successional species to new areas (Ehrlich 1996; Matlack 1994; Meier et al. 1995). Though dispersal efficiency has long been theorized to determine the rate at which a species will colonize new habitats, little empirical data for woodland herbaceous species exists (Beatty 1984; Matlack 1994; MacArthur and Wilson 1963; Thompson 1980). Matlack's (1994) comparison of species-rich old-"regrowth" (a term used by the author to acknowledge the probability of small-scale selective cutting in these forests by native peoples) and species-poor successional stands in the Delaware/Pennsylvania Piedmont zone stands out. Matlack measured migration rates between contiguous areas and found many species with extremely low to no measurable rates at all, leading him to warn that such characteristics "threaten [these species]

continued existence in the second-growth forest landscape" (Matlack 1994, p. 1491). Significant differences in rates of migration were based on dispersal modes, with ingested and adhesive seeds dispersing the most efficiently, wind-dispersed seeds proving the next most efficient, and ant- or gravity-dispersed seeds migrating least efficiently. Successional stands were particularly species-poor in ant-, spore- and gravity-dispersed species, species shown to be important to late-successional floras (Handel et al. 1981). Other studies, such as that of the dispersal of *Panax trifolius* drupes (Meier et al. 1995), concur with Matlack's findings.

Dependence upon specific microhabitats for seed germination, such as decayed logs, canopy gaps or duff pockets, may complicate the difficulties late-successional species face in colonizing new areas.

IV. Species differences found in this study

In this study, the majority of the species lacking in secondary study sites were herbaceous species with relationships to microhabitats or resource conditions which have been cited as deficient in regrowth conditions. The small scale of this study dictates caution in the extrapolation of specific findings. None of the species found here to exclusively (or more abundantly) occur in old-growth sites should be considered "old-growth species." Rather, it is patterns in the types of taxa, or uniting and limiting characteristics of these taxa, which should be of interest.

a. Species of wet soils. The RCB ANOVA analysis comparing differences in the number of species associated with wet soils in old- versus secondary-growth study sites

very closely approached statistical significance. Cluster analysis using these species separated secondary sites from old-growth sites in two agglomerations. Species associated with wet soils accounted for 34.5% of the 55 species unique to old-growth study sites. By contrast, only 5.9% of the 17 species unique to secondary-growth sites and 13.3% of the 75 species found in both old-growth and secondary sites were species of wet microhabitats. It was also noted that many of the species of particularly lower abundance in secondary sites, relative to old-growth sites, were species associated with wet soils, such as *Cicaea alpina, Chrysosplenium americanum, Gymnocarpium dryopteris, Viola* and *Galium* species.

Several other studies have noted species of wet habitats as specifically vulnerable to extirpation in post-harvest environments (Meier et al. 1995, Roberts and Zhu 2002; Rooney and Dress 1997). Mou et al. (1993) reported changes in hydrology patterns of clearcut areas and commented that rutting and erosion could inhibit future recovery of forest floor species. While not statistically conclusive, the results presented here strongly suggest that the old-growth sites of this study contained more wet microhabitats than their secondary counterparts.

b. Species of moist and/or rich soils. While RCB ANOVA results comparing the number of species associated with moist and/or rich soils in old- versus secondary-growth study sites found no statistically significant differences, TWINSPAN and cluster analysis grouped secondary sites in two steps using these species. Species associated with moist and/or rich forest soils accounted for 27.3% of the 55 species unique to old-growth study sites and 30.7% of the 75 species found in both old-growth and secondary sites. By

contrast, only 23.5% of the 17 species unique to secondary-growth sites were species requiring similar conditions. Together, species reliant on moist to wet soils accounted for 61.8% of species unique to old-growth sites, 44% of species occurring in both forest types, and 29.4% of species unique to secondary sites. These results strongly suggest that the old-growth sites of this study contained moister, richer soils, and more wet microhabitats than their secondary counterparts.

c. Species of dry and/or disturbed soils. No statistically significant results were obtained in any analyses using richness and/or abundance data of species associated with dry and/or disturbed soils. Yet, these species accounted for 41.2% of the species unique to secondary-growth sites. By contrast, only 9.1% of species unique to old-growth study sites and 4.0% of species found in both old-growth and secondary sites were species associated with similar conditions. These results may be an artifact of small sample size, as B-m was contained a disproportionately large number of the species under discussion than either other secondary-growth site. It is also possible that these results show a patchiness of soil conditions within secondary sites, such that areas of dry soils represent specific microhabitats within the larger landscape. Theoretically, these areas may be exhibiting more severe and long-term impacts due to harvesting and altered moisture regimes. More study is needed regarding soils conditions and moisture regimes in secondary versus old-growth forests.

d. Rare and unique species. The flora of secondary-growth sites in this study showed significantly fewer rare and infrequently occurring species, as well as significantly fewer unique species, concurring with the findings of Halpern and Spies (1995), Meier et al. (1995), and Roberts and Zhu (2002). One reason rare species have been found to be more susceptible to extirpation in logged forests is increased odds of total population loss during disturbance events (from Spiller and Schoener 1998). Another reason is that small distributions may indicate species limited to certain vulnerable microhabitats. Both explain why rare species have been considered by some to be among the better indicators of primary forests (Peterken and Game 1984; Spies 1991; Whitney and Foster 1988).

The results of this study strongly suggest that rare and infrequently occurring, predominantly herbaceous species are good indicators of old-growth systems. Although not specifically measured, this pattern of apparent loss of species of small population size is seen as a verification of the secondary-growth sites' reduction in microhabitats and "patchy" conditions, resulting at least in part, from the loss of gap-phase dynamics. For instance, in this study 71.3% of the occurrences of species reliant on wet microhabitats were ranked as rare or infrequent. It remains unclear whether the sites' initial clearing may also have resulted in the destruction of microhabitats. This study's findings suggest that rare and infrequently occurring species of wet microhabitats may be particularly indicative of old-growth floristic conditions.

Loss of species of small population size (species reliant on microhabitats) most likely also resulted in a loss of unique species in secondary sites. In old-growth sites, 71.4% of the 55 unique species were rare and infrequently occurring species; in

secondary sites, 74.3% of the 17 unique species were similarly low in abundance.

e. Species limited by life-history characteristics

Though issues of morphology and physiology were explored for the species in this study, few important trends were recognized. Little species-specific data for herbaceous species in temperate forests exists (Beatty 1984; Matlack 1994; MacArthur and Wilson 1963; Thompson 1980). The following is a brief synopsis of the findings:

Personal observation, a search of the literature, and a review of species collections in the Hodgdon Herbarium (University of New Hampshire) revealed that most of the species unique to old-growth sites in this study were at least somewhat to vigorously clonal (*Anemone quinquifolia, Dryopteris campyloptera, Carex scabrata, Cerastium arvense, Mitella nuda, Osmunda claytoniana, Scutellaria lateriflora, Solidago macrophylla, Carex deflexa*, etc.), yet several species unique to secondary-growth sites also displayed this trait (*Pteridium aquilinum, Solidago rugosa, Lycopodium clavatum, Viburnum nudum*). A higher percent of the species unique to secondary-growth sites were observed to be high seed producers (*Amelanchier laevis, Carex* spp., *Ribes glandulosum, Spiraea tomentosa, Solidago rugosa subsp. rugosa),* though species unique to old-growth sites were by no means universally infertile (*Carex scabrata, Solidago macrophylla, Cardamine pensylvanica, Euthamia graminifolia, Eupatorium rugosum, Ribes laucustre,* etc.). Modes of dispersal seemed evenly mixed between the two groups (Ridley 1930), but when habitat requirements were considered, many wind- or animal-dispersed species in old-growth sites (the most efficient modes for migration, according to Matlack1994) were limited by the need for suitable (i. e., moist to wet) habitat which was not prevalent

in secondary sites.

Overall, limitations of habitat and soil moisture remain the strongest indicators of the distinction between species of old- and secondary-growth forests.

f. Vernal herbaceous species. It has been suggested that vernal herbaceous species may be useful diagnostic indicators of disturbance and subsequent recovery of eastern forest systems from the effects of tree harvesting (Duffy and Meier 1992; Goebel et al. 1999; Keddy and Drummond 1996; Meier et al. 1995). Altered competitive dynamics and loss of habitat have been noted as possible factors in the extirpation of these species as the result of clearcutting. Limiting life-history characteristics and long-term changes in microenvironment have been hypothesized to repress recovery and inhibit migration to secondary sites. Bratton (1976) and Meier et al. (1995) commented that vernal species in particular may be more sensitive to issues of substrate, relying on soil organic matter, duff pockets and logs in various stages of decay for habitat. Rogers (1982) found lower importance value of vernal herbaceous species correlated with places of nutrient-poor mineral soils. While vernal species are probably not gap species *per se* (Moore and Vankat 1986; Rogers 1982), patterns in the forest floor produced by gap processes over the long-term may foster or maintain diversity in this community. A better understanding is needed regarding the issues governing distributions of these species.

Seven of the 55 species unique to old-growth sites (12.7%) were vernal herbaceous species, while only one of the 17 species unique to secondary-growth sites (5.9%) were spring blooming herbs (25.3% of the species in common to both forest types were vernal). Within this list, three spring ephemeral species were found only in old-

growth sites (*Arisaema triphyllum, Claytonia caroliniana, Dicentra cucullaria);* no spring ephemeral species were unique to secondary sites.

While the secondary sites in this study noticeably clustered using the vernal species, ANOVA results for this subset of the flora were not significant. This seeming disagreement with the literature may be an artifact of small sample size, as Shingle Pond's vernal species list was notably depauperate. Shingle Pond's greater mean vernal floristic similarity to the secondary-growth sites was corroborated by cluster analysis, which grouped this old-growth site closer to the secondary than old-growth cluster (Figure 13). It is alternatively possible that vernal herbaceous species (as well as spring ephemeral species importance) may have a lower importance value in New England forests than in cove forests of the Appalachian Mountains, where previous studies have been conducted. Fewer vernal species in both old-growth and secondary-growth floras overall may explain the lack of significance. While infrequent, ice storm event such as that of 1998 do occur in these northern states and therefore effect old- as well as secondary-growth canopies to some real extent. It is therefore not possible to positively ascertain from this study the relationship between vernal herbaceous species in old- versus secondary-growth forest types in New England temperate forests.

SUMMARY

This study concurs with the findings of Duffy and Meier (1992) and Goebel et al. (1999) in detecting significant floristic differences between eastern old-growth forests and mid-successional secondary-growth forests recovering from the effects of timber harvesting. Old-growth floras were significantly richer in herbaceous species, specifically woodland herbaceous species, and these species showed significantly different abundance distributions relative to secondary floras. Old-growth floras included more species of small population size and were also significantly richer in unique herbaceous species. Differences in the number of species associated with various soil moisture regimes in some cases closely approached statistical significance.

While not directly measured, the lack of gap-phase dynamics in the canopy and changes in hydrology and soil moisture as the result of harvesting events are hypothesized as the primary explanation for these results. Insufficient life-history data on the species in this study made it impossible to assess the importance of this factor.

Canopy gaps in eastern old-growth forests may alter birth and death rates of the species present by providing microhabitats with altered resource conditions, reducing competitive exclusion, and increasing rates of growth and reproduction. Gap dynamics may influence the pattern of immigrations and extinctions, as large gaps provide opportunities for new species to colonize the stand, and small gaps may reduce extirpation risks of pre-existing species by offering reproductive niches that enrich the seed bank. In order to increase diversity, mid-successional forest ecosystems rely heavily

on species that are likely among the least efficient migrators. Life-history traits of many late-successional species make them slow to spread and/or colonize secondary forests and the lack of gap-phase dynamics, distance from source pools, and possibly altered soil conditions in these disturbed areas may further impede understory reestablishment.

There has been insufficient recovery time as yet in eastern U. S. forests to judge the length of time necessary for mid-successional forests to attain the species diversity of old-growth systems, but the data indicate that 90-100 years is insufficient. Actual recovery periods may be closer to the average lifespan of the system's dominant tree species.

LIMITATIONS OF THE STUDY

1. This study suffers the same limitations as all chronosequences in that it is unlikely that any two sites are exact environmental replicants of one another. The design of this study aimed to minimize these discrepancies, but characteristics such as pH, soil moisture, and cation exchange capacity (CEC) were not directly measured and may have had effects on understory species compositions.

2. Site history data prior to 1914 for the secondary sites were imperfect and sometimes consisted of anecdotal information. Although it seems unlikely (for the reasons expressed in Site Descriptions), it is possible that the secondary-growth matches for the Bowl and Lafayette Brook were initially coniferous and not hardwood stands when they were logged in the late 19^{th} and early 20^{th} centuries. If so, seed bank and soil differences may have contributed to differences in species richness at these sites.

3. While every attempt was made within the limitations of this study to closely match the environmental factors of old-growth sites with those of secondary sites, slope-aspects were not exactly the same. These discrepancies were judged to be acceptable, but it should be noted that aspect has been shown to have significant effect on species composition.

4. Care should be taken in extrapolating results of this study to modern methods of forest

harvesting. This study, like all studies of 70-100 year old secondary forests in the U.S., is actually examining the effects of now-antiquated logging techniques. Modern methods of harvesting did not begin in the National Forests until around 1964 (Johnson et al.1993). It is generally assumed that contemporary methods more severely affect forest systems, as before this time harvesting was largely unmechanized, highly variable and probably more like series of selective cuts (Metzger and Schultz 1981).

MANAGEMENT IMPLICATIONS

Results of this study concur with the research of Goebel et al. (1999), Kimball et al. (1995), Meier et al. (1995) and others in recommending that future harvesting techniques mimic the natural gap dynamics of old-growth forests as closely as possible in order to maintain species diversity. The practice of "high grading" (in which single trees of exceptional value are removed) and carefully applied selective cutting may be applicable practices, but more research is needed. Appropriate gap sizes and their distributions within different forest types need more scientific attention.

In addition to breaks in the canopy, attention should be paid to the amount of CWD contributed to the forest floor and its placement, which may be important in terms of interruption of surface drainage patterns (see pp. 64). More study is needed regarding soil moisture regimes and hydrological patterns in old- versus secondary-growth forest systems.

Metzger and Schultz (1981) found the flora of Michigan forests that had been selectively cut several times over a 50 year period to be more diverse than areas clearcut 50 years ago, suggesting that repetitive intermediate disturbance safeguards species diversity more effectively than does intense disturbance followed by a period of rest. To this end, it should be understood that clearcutting disrupts forest ecosystems and species composition for likely well over the 120 year rotation time afforded managed hardwood forests in the WMNF under the best of conditions. It is therefore likely that rotation times for eastern deciduous forests should be lengthened. Though many of the most vulnerable

herbaceous species may already be lost, the same mechanisms which contribute to species losses in harvested primary forest remain at issue when secondary forests are harvested. Practices that reduce soil disruption, compaction, erosion and damage to understory species should be pursued.

Bormann and Likens' (1979) statistics on catastrophic disturbance cycles in eastern temperate deciduous forests implied that, without human disturbance, approximately 20% of the landscape would be covered by first-generation stands, while the remaining 80% would be composed of mostly trees at or near their maximum age. Today, less than 1% of the landscape in the eastern U.S. (4% of forested land) is primary forest (Davis 1996). While silvicultural practices can and should be amended in order to promote diversity, the questionable recovery rates of many late-successional species make the preservation of existing old-growth forests critical. While large areas may be necessary to maintain regional and global diversity, Meier et al. (1995) found no correlation between area and mean number of species per m^2 for the old-growth preserves they examined, suggesting *refugia* of any size are valuable as source pools at the landscape level. Matlack (1994) found understory richness in contiguous as well as separate successional stands limited by distance to source pools, and that stands isolated from these propagule sources suffered significantly lower species richness.

Species-specific studies, including research on growth rates, reproductive and dispersal abilities, and immigration and extinction potentialities of woodland species in response to disturbance, are badly needed. In order to minimize the likelihood that rare species will be overlooked, more complete inventories should be conducted on areas both before and after harvesting events, using the methodology of this study. More inventories

of old-growth areas and long-term monitoring of the flora within should be a priority until such time as the equivalent species diversity is restored to secondary forests.

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Appendix A. Abundance checklist of the vascular flora for the six study sites: The Bowl RNA, Shingle Pond (SP), Lafayette Brook Scenic Area (LB), Bowl- match (Bm), Shingle Pond-match (SPm), and Hubbard Brook Experimental Forest Watershed 6 (W6). Hubbard Brook data from Teeling (1998). Abundance modified from Palmer et al. (1995). Nomenclature follows Kartesz (1994). Species are designated (D) as woodland herbaceous species[w], vernal herbaceous species[v], associated with moist and/or rich soils*, associated with wet soils**, associated with dry and/or disturbed soils[d],.

	D	Bowl	SP	LB	Bm	SPm	W6
PTERIDOPHYTA							
Dennstaedtiaceae (Hay-Scented Fern Family)							
Dennstaedtia punctilobula (Michx.) Moore.	w	1	3	1	2	3	3
Pteridium aquilinum (L.) Kuhn.	d				3	3	
Dryopteridaceae (Wood Fern Family)							
Athyrium thelypteroides (Michx.) Desv.	w *	4			2	3	
Athyrium filix-femina var. *angustum* (Willd.) G. Lawson	w *	2	2	3		2	1
Dryopteris campyloptera Clarkson [=Dryopteris spinulosa var. americana (Fisch.) Fern.]	w *	4	1	3			
Dryopteris carthusiana (Vill.) H.P. Fuchs [=Dryopteris spinulosa (O.F. Muell.) Watt; D. austriaca var. spinulosa (O.F. Muell.) Fisch.]	w					2	1
Dryopteris boottii (Tuckerman) Underwood [= Dryopteris cristata (L.) Gray x Dryopteris intermedia (Muhl.)]	w	4	4			3	
Dryopteris intermedia (Muhl. ex Willd.) Gray	w	2	4	4	2		4
Dryopteris marginalis (Linnaeus)	w	1					
Gymnocarpium dryopteris (L.) Newm.	w **	2	1	4	1	1	
Polystichum acrosticoides (Michx.) Schott.	w	1		2			
Onoclea sensibilis L.	w **		1			2	
Lycopodiaceae (Clubmoss Family)							
Huperzia lucidula (Michx.) Trevisan [=Lycopodium lucidulum Michx.]	w	5	2	3	3	3	5
Lycopodium annotinum L.	w			2		3	
Lycopodium clavatum L.	w d				3		
Lycopodium obscurum L	w *			1	3	3	

	D	Bowl	SP	LB	Bm	SPm	W6
Ophioglossaceae (Adder's Family)							
Botrychium oneidense (Gilbert) House	w *						1
Botrychium simplex E. Hitchc.	w *		1				
Osmundaceae (Royal Fern Family)							
Osmunda cinnamomea L.	w **		2	2	2	3	
Osmunda claytoniana L.	w *		1				
Polypodeaceae (Polypody Family)							
Polypodium virginianum L.	w	3		4		2	
Thelypteridaceae (Marsh Fern Family)							
Phegopteris connectilis (Michx.) Watt [=Thelypteris phegopteris (L.) Slosson]	w *	2	1	3	3	3	4
Thelypteris noveboracensis (L.) Nieuwl.	w	1	1	3	3	3	2
GYMNOSPERMS PINOPHYTA							
Pinaceae (Pine Family)							
Abies balsamea (L.) P. Mill.		2	1	3	2	2	2
Picea rubens Sarg.		3	2	2	2	2	2
Pinus resinosa Ait.	d				1		
Pinus strobus L.				1	2	2	
Tsuga canadensis (L.) Carr.	*	1	2	2	3	3	1
Taxaceae (Yew Family)							
Taxus canadensis Marsh.			1				1
ANGIOSPERMS MAGNOLIOPHYTA MAGNOLIOPSIDA							
Aceraceae (Maple Family)							
Acer pensylvanicum L.		5	4	4	3	4	2
Acer rubrum L.		2	2	2	2	2	2
Acer saccharum Marsh.		5	5	5	5	5	4
Acer spicatum Lam.	*	2	1	3	3	3	2
Aquifoliaceae (Holly Family)							
Ilex verticillata (L.) Gray	**		1			1	
Nemopanthus mucronatus (L.) Loes.	**			1			
Araliaceae (Ginseng Family)							
Aralia nudicaulis L.	w	4	5	2	4	4	3
Aralia racemosa subsp. *racemosa* L.	w *		4				
Panax trifolius L.	w v *			1			1

	D	Bowl	SP	LB	Bm	SPm	W6
Asteraceae (Aster Family)							
Aster acuminatus Michx.	w	4	5	3	3	4	3
Aster macrophyllus L.	w d			1			
Aster lanceolatus Willd.	w *	2					
Aster sp. 1			1				
Aster sp. 2				1			
Cirsium Miller			1				
Erechtites hieraciifolia (L.) Raf. var. *hieraciifolia*	w d		1		1		
Erigeron strigosus Muhl.	d		1				
Eupatorium rugosum Houttuyn.	w *	4					
Euthamia graminifolia (L.) Nutt.	*	3	1		2		
Prenanthes altissima L.	w	2	2	2	1	2	2
Solidago canadensis L. var. *canadensis*	w		2				
Solidago macrophylla Pursh	w *	2		1			
Solidago rugosa P. Mill. subsp. *rugosa* var. *rugosa*	d				2	2	
Taraxacum officinale G.H. Weber ex Wiggers	d		1				
Balsaminaceae (Touch-me-not Family)							
Impatiens capensis Meerb.	w **	3					
Betulaceae (Birch Family)							
Betula alleghaniensis Britt.		5	2	3	2	2	4
Betula cordifolia Regel [=Betula papyrifera var. cordifolia (Regel) Fern.]		2		3			2
Betula papyrifera Marsh.		2		3	3	3	
Corylus americana Walter				1			
Ostrya virginiana (P. Mill.) K. Koch.						1	
Brassicaceae (Mustard Family)							
Cardamine pensylvanica Muhl.	w **	2	1				
Caprifoliaceae (Honeysuckle Family)							
Diervilla lonicera P. Mill.	*		3	1	2		
Lonicera canadensis Bartr. ex Marsh.		1	3	3	3	2	3
Sambucus racemosa subsp. *pubens* var. *pubens* (Michx.) Koehne	*	3	3	3	2	2	3
Viburnum alnifolium Marsh. [=Viburnum lantanoides Michx.]		5	5	5	5	5	5
Viburnum nudum var. *cassinoides* (L.) T. & G.	*					3	
Caryophyllaceae (Pink Family)							
Cerastium arvense L.	d		1				
Cornaceae (Dogwood Family)							
Cornus alternifolia L. f.	*	3	2	2	1	1	1
Cornus canadensis L.	w v *			2			

	D	Bowl	SP	LB	Bm	SPm	W6
Ericaceae (Heath Family)							
Epigaea repens L.	w v d				1		
Gaultheria hispidula (L.) Muhl. ex Bigelow	w			1			
Vaccinium angustifolium Ait.			1				
Fagaceae (Beech Family)							
Fagus grandifolia Ehrh.		5	5	4	5	5	4
Quercus rubra L.						2	
Fumariaceae (Fumatory Family)							
Dicentra cucullaria (L.) Bernh.	w v *	2					
Grossulariaceae (Gooseberry Family)							
Ribes lacustre (Pers.) Poiret.	**	2		2			
Ribes glandulosum Grauer	**						1
Labiatae (Mint Family)							
Lycopus uniflorus Michx.	w **		3				
Scutellaria lateriflora L.	w **		2				
Monotropaceae (Indian Pipe Family)							
Monotropa uniflora L.	w *	1	1	2	2	1	2
Oleaceae (Olive Family)							
Fraxinus americana L.	*	1	4			3	3
Onagraceae (Evening Primrose Family)							
Circaea alpina L.	w **	3	3	2		2	
Epilobium ciliatum var. *ciliatum* Raf.	w **		2				
Epilobium glandulosum Lehm.	w **	2	2				
Orobanchaceae (Broom-rape Family)							
Epifagus virginiana (L.) W. Bart.	w	1	1		2	3	1
Oxalidaceae (Wood-sorrel Family)							
Oxalis acetocella L.	w v *	5	3	4	2	3	4
Portulacaceae (Purslane Family)							
Claytonia caroliniana Michx. var. *caroliniana*	w v *	1		3			
Primulaceae (Primrose Family)							
Trientalis borealis Raf.	w	3	1	4	4	4	3
Pyrolaceae (Shinleaf Family)							
Pyrola elliptica Nutt.	w	2	3			4	
Pyrola rotundifolia L.	w		2				

	D	Bowl	SP	LB	Bm	SPm	W6
Ranunculaceae (Buttercup Family)							
Actaea pachypoda Ell.	w *	2	3				
Actaea rubra (Ait.) Willd.	w *	2					
Anemone quinquefolia L.	w v *	2					
Coptis trifolia subsp. *groenlandica* (Oeder) Hultén	w v *			4	1		
Thalictrum pubescens Pursh [= T. polygamum Muhl.]	w **	3		1			
Rosaceae (Rose Family)							
Amelanchier laevis Wieg.	d				3	3	
Prunus pensylvanica L. f.	d	1	2	2	2	1	
Rubus elegantulus Blanch.	d	1					
Rubus idaeus subsp. *strigosus* (Michx.) Focke	d	1	3	2		2	2
Rubus pubescens Raf.	w *	2	1	3	2	3	
Sorbus americana Marsh.	*	2	3	3		1	
Spiraea tomentosa L.	*						1
Rubiaceae (Madder Family)							
Galium asprellum Michx.	w **		3	1	1	1	1
Galium circaezans Michx.	w **	2					
Galium triflorum Michx.	w **	3					
Mitchella repens L.	w v	1	1		3	3	2
Salicaceae (Willow Family)							
Populus grandidentata Michx.	d					2	
Saxifragaceae (Saxifrage Family)							
Chrysosplenium americanum Schwein. ex Hook.	w v **	4	2				1
Mitella nuda L.	w v **	1					
Tiarella cordifolia L.	w v *			4			
Scrophulariaceae (Figwort Family)							
Chelone glabra L.	w **	3	2				
Tiliaceae (Linden Family)							
Tilia americana L.	*		3				
Violaceae (Violet Family)							
Viola cucullata Ait.	w v **	3	3	2		3	
Viola macloskeyi subsp. *pallens* (Banks ex DC.) M.S.Baker	w v **	3	4	2	1	2	2
Viola rotundifolia Michx.	w v	4		2		2	2

	D	Bowl	SP	LB	Bm	SPm	W6
LILIOPSIDA (Monocotyledons)							
Araceae (Arum Family)							
Arisaema triphyllum (L.) Schott subsp. *triphyllum*	w v **			1			
Cyperaceae (Sedge Family)							
Carex arctata Boott ex Hook.	w *	2	2	1	3	3	1
Carex brunnescens (Pers.) Poir.	w *	1	2	1	3	2	
Carex communis Bailey	w		1	3	3	2	
Carex debilis Michx.				3			
Carex deflexa Hornem.	**		2	3			
Carex gynandra Schwein.	w **	2		1			1
Carex intumescens Rudge	w *	1	1	3			2
Carex leptonervia (Fern.) Fern.	w	2					
Carex scabrata Schwein.	w **	2	2	2			
Carex sp. 1						2	
Carex sp. 2						1	
Liliaceae (Lily Family)							
Clintonia borealis (Ait.) Raf.	w v	4	2	4	2	3	4
Erythronium americanum Ker-Gawl.	w v	5		4	2		4
Maianthemum canadense Desf.	w v	3	2	4	4	4	3
Medeola virginiana L.	w v *	4	4	3	3	3	4
Polygonatum pubescens (Willd.) Pursh	w v *		3	2			1
Smilacina racemosa (L.) Desf.	w *		3	3	2	2	3
Streptopus amplexifolius (L.) DC.	w v *	2		1	1	1	
Streptopus roseus Michx.	w v	4	2	3	3	3	3
Trillium erectum L.	w v	3	3	2	3	3	3
Trillium undulatum Willd.	w v	2	3	2	3	3	2
Uvularia sessilifolia L.	w v	5	5	4	4	3	4
Veratrum viride Ait.	w **	1					
Orchidaceae (Orchid Family)							
Cypripedium acaule Ait.	w v	1	1	2	2	1	
Goodyera repens (L.) R. Br. ex Ait. f.	w		2				
Habenaria orbiculata (Pursh) Torr. [=Platanthera orbiculata (Pursh) Lindl.]	w *						1
Poaceae (Grass Family)							
Brachyelytrum erectum (Schreber) P. Beauv. var. septentrionale	w *		1	2	2	2	
Cinna latifolia (Trevir.) Griseb.	w *	2	1				3
Glyceria melicaria (Michx.) F. T. Hubbard	**	3					
Unknown sp. 1				1			
Unknown sp. 2		3					
Unknown sp. 3		2					

Appendix B. Complete and unaltered TWINSPAN two-way ordered table for the total flora, based on ranked abundance values of 147 species (only 100 species are output in the table). Order of the six samples (sites) is 3 Lafayette Brook, 4 Bowl-match, 5 Shingle Pond-match, 6 HBEF W6, 1 The Bowl, 2 Shingle Pond.

345612

30 *Carex debilis* 4----- 000000

134 *Tiarella cordifolia* 5----- 000000

46 *Coptis trifolia* var. *groenlandica* 52---- 000001

82 *Lycopodium annotinum* 3-4--- 00001

97 *Panax trifolius* 2--2-- 00001

55 *Dryopteris carthusiana* --32-- 000100

8 *Amelanchier laevis* -44--- 000101

83 *Lycopodium clavatum* -4---- 000101

111 *Pteridium aquilinum*-44--- 000101

125 *Solidago rugosa* ssp. *rugosa* -33--- 000101

84 *Lycopodium obscurum* 244--- 00011

101 *Pinus strobus* 233--- 00011

93 *Osmunda cinnamomea* 334--3 00100

98 *Phegopteris connectilis* 444532 00100

122 *Smilacina racemosa* 4334-4 00100

133 *Thelypteris novaboracensis* 444322 00100

136 *Trientalis borealis* 555442 00100

22 *Betula papyrifera* 444-3- 001010

25 *Brachyelytrum septentrionale* 333--2 001010

29 *Carex communis* 443--2 001011

88 *Mitchella repens* -44322 0011

50 *Cypripedium acaule* 332-22 010000

128 *Streptopus amplexifolius* 222-3- 010000

1 *Abies balsamea* 433332 010001

5 *Acer spicatum* 444332 010001

27 *Carex arctata* 244233 010001

45 *Clintonia borealis* 534553 010001

51 *Dennstaedtia punctilobula* 234424 010001

65 *Erythronium americanum* 53-56- 010001

70 *Galium asprellum* 2222-4 010001

78 *Huperzia lucidula* 444663 010001

81 *Lonicera canadensis* 443424 010001

86 *Maianthemum canadense* 555443 010001

90 *Monotropa uniflora* 332322 010001

119 *Rubus pubescens* 434-32 010001

129 *Streptopus roseus* 444453 010001

138 *Trillium undulatum* 344334 010001

139 *Tsuga canadensis* 344223 010001

143 *Viburnum alnifolium* 666666 010001

2 *Acer pensylvanicum* 545365 010010

3 *Acer rubrum* 33-333 010010

4 *Acer saccharum* 666566 010010

10 *Aralia nudicaulis* 355456 010010

13 *Aster acuminatus* 445456 010010

18 *Athyrium filix-femina* 4-3233 010010

20 *Betula allegheniensis* 433563 010010

32 *Carex gynandra* 2--23- 010010

47 *Cornus alternifolia* 322243 010010

56 *Dryopteris intermedia* 53-535 010010

68 *Fagus grandifolia* 566566 010010

87 *Medeola virginiana* 444555 010010

96 *Oxalis acetocella* 534564 010010

99 *Picea rubens* 333343 010010

109 *Prenanthes altissima* 323333 010010

110 *Prunus pensylvanica* 332-23 010010

118 *Rubus idaeus* ssp. *strigosus* 3-3324 010010

120 *Sambucus racemosa* ssp. *pubens* 433444 010010

137 *Trillium erectum* 344444 010010

140 *Uvularia sessilifolia* 554566 010010

147 *Viola rotundifolia* 3-335- 010010

19 *Athyrium thelypteroides* -34-5- 010011

28 *Carex brunnescens* 243-23 010011

33 *Carex intumescens* 4--322 010100

76 *Gymnocarpium dryopteris* 522-32 010100

21 *Betula cordifolia* 4--33- 010101

106 *Polypodium virginianum* 5-3-4- 010101

44 *Claytonia caroliniana* 4---2- 01011

107 *Polystichum acrostichoides* 3---2- 01011

59 *Epifagus virginiana* -34222 0110

92 *Onoclea sensibilis* --3--2 0110

69 *Fraxinus americana* --4425 01110

79 *Ilex verticillata* var. *verticillata* --2--2 01110

63 *Erichtites hieraciifolia* -2---2 01111

41 *Cinna latifolia* ---432 1000

58 *Dryopteris boottii* --4--5 1000

146 *Viola macloskeyi* var. *pallens* 323345 1000

112 *Pyrola elliptica* --5-34 1001

126 *Sorbus americana* 4-2-34 1010

145 *Viola cucullata* 3-4-44 1010

105 *Polygonatum pubescens* 3--2-4 1011

116 *Ribes lacustre* 3---3- 1011

31 *Carex deflexa* 4----3 110

35 *Carex scabrata* 3---33 11100

54 *Dryopteris campyloptera* 4---52 11100

132 *Thalictrum pubescens* 2---4- 11100

42 *Circaea alpina* 2-3-44 111010

124 *Solidago macrophylla* 2---34 111010

53 *Diervilla lonicera* 23--54 111011

6 *Actaea pachypoda* ----34 1111

11 *Actaea rubra* -----5 1111

26 *Cardamine pennsylvanica* ----32 1111

39 *Chelone glabra* ----43 1111

40 *Chrysosplenium americanum* ---253 1111

62 *Epilobium glandulosum* ----33 1111

66 *Eupatorium rugosum* ----5- 1111

67 *Euthamia graminifolia* ----42 1111

72 *Galium triflorum* ----4- 1111

74 *Glyceria melicaria* ----4- 1111

80 *Impatiens capensis* ----4- 1111

85 *Lycopus uniflorus* -----4 1111

000011

0111