

BIOLOGY 208 - POPULATION AND COMMUNITY BIOLOGY
SNYDER-MIDDLESWARTH STATE PARK NATURAL AREA
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Introduction

Old-growth forests have become increasingly rare in North America since the time of European colonization and today represent a tiny fraction of the total forested area of the eastern United States (Nowacki and Abrams 1994, Rooney 1995, Orwig and Abrams 1999). Old-growth forest is particularly rare in central Pennsylvania because of intensive logging for timber and charcoal production during the past 150 years (Nowacki and Abrams 1991, Abrams and Orwig 1996). As a consequence, eastern old-growth forest, and Pennsylvania old-growth forest in particular, exist in small stands that are isolated from other old-growth forests by an intervening matrix of successional forests (Smith 1989, Farr and Tyndall 1992, Tyrrell and Crow 1994).

The 500-acre (200-ha) Snyder-Middleswarth Natural Area within the Bald Eagle State Forest includes one of the few stands of old-growth forest remaining in Pennsylvania and is among the largest such stands existing within Pennsylvania state forests (Pennsylvania Bureau of Forestry). Five tree species dominate the Snyder-Middleswarth landscape including eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), black birch (*Betula lenta*), red maple (*Acer rubrum*) and chestnut oak (*Quercus montana*). Two additional tree species, eastern white pine (*Pinus strobus*) and striped maple (*Acer pensylvanicum*), are present but are far less common. The dominant tree species are visibly segregated within this forest owing to the environmental and edaphic variation ranging from the Swift Run bottomlands to the slopes and ridge tops, the adaptations of species to subsets of environmental and edaphic conditions, differential exposure to wind and storm events, and the years of competitive interactions among species (Zawadzka and Abrahamson 2003).

The old-growth forest is located in a narrow and steep ravine between two ridges that run east to west; Buck Mountain lies to the north and Thick Mountain to the south. The ravine, created by Swift Run, has well-developed north-facing and south-facing slopes as well as a bottomland. Elevations in the area range from 1480 ft to 1800 ft (450 m to 550 m), with slopes varying in steepness from 1-68%. The predominant soils are extremely stony and sandy well-drained loams that have weathered from sandstone and shale and have low to moderate available water capacity (Eckenrode 1985).

Thanks originally to the inaccessibility of this ravine and in 1965 to its preservation as a *National Natural Landmark*, a 330-acre (135-ha) portion of this forest has never been logged. The extent of direct human impact to the area is a footpath that runs along the northern bank of Swift Run and loops back along the north-facing slope. Hunting of deer and other game is allowed in the adjoining state forestlands.

There have been many natural disturbances within this old-growth forest during the past three decades (Abrahamson, personal observation). Windstorms, especially those associated with snow or ice events, have toppled a number of the larger hemlock and yellow birch throughout the stand. Furthermore, the crowns of slope and ridge top trees frequently show evidence of wind and/or ice damage. Gypsy moth outbreaks have occurred periodically within central Pennsylvania since the mid-1970s and have markedly impacted the oak canopies within the area during one or two growing seasons.

Species Distributions

Of the seven tree species, eastern hemlock has the highest relative importance (48%), followed by black birch (14%), yellow birch (13%), chestnut oak (11%), and red maple (11%). Striped maple (2%) and eastern white pine (1%) have much lower importance values (Zawadzka and Abrahamson 2003). These average values, however, do not adequately represent the variations in the distributions of species observed in the bottomland, on the slopes, or ridge tops. For example, the southern Thick Mountain ridge top is dominated by hemlock and black birch while the bottomland is composed of hemlock and yellow birch and the northern Buck Mountain ridge top is principally chestnut oak and red maple (Table 1).

Table 1. Density, frequency, dominance and relative density, frequency, dominance and importance for woody stems (> 6 cm dbh) from five topographic transects sampled within the Snyder-Middleswarth Natural Area (Zawadzka and Abrahamson 2003).

Species	Density (stems/ha)	Frequency (% quads)	Dominance (m ² /ha)	Relative Density	Relative Frequency	Relative Dominance	Relative Importance
Thick Mountain Southern Ridge Top							
Eastern Hemlock	1,075.0	100	49.5	77.8	48.5	77.8	68.0
Black Birch	268.8	75	11.2	19.5	36.4	17.6	24.5
Red Maple	25.0	19	2.5	1.8	9.1	4.0	5.0
Yellow Birch	12.5	13	0.4	0.9	6.1	0.6	2.5
Totals	1,381.3	206	63.6	100.0	100.0	100.0	100.0
North-facing Slope							
Eastern Hemlock	618.8	100	51.3	66.9	44.4	78.8	63.4
Black Birch	168.8	63	6.8	18.2	27.8	10.5	18.8
Yellow Birch	125.0	50	5.0	13.5	22.2	7.7	14.5
Red Maple	12.5	13	2.0	1.4	5.6	3.0	3.3
Totals	925.0	225	65.1	100.0	100.0	100.0	100.0
Bottomland							
Eastern Hemlock	381.3	100	28.3	52.6	51.6	53.3	52.5
Yellow Birch	343.8	94	24.8	47.4	48.4	46.7	47.5
Totals	725.0	194	53.1	100.0	100.0	100.0	100.0
South-facing Slope							
Eastern Hemlock	275.0	94	26.0	51.2	39.5	65.9	52.2
Chestnut Oak	87.5	44	4.2	16.3	18.4	10.6	15.1
Red Maple	62.5	44	3.5	11.6	18.4	8.9	13.0
Black Birch	50.0	38	3.5	9.3	15.8	8.8	11.3
Yellow Birch	62.5	19	2.3	11.6	7.9	5.9	8.4
Totals	537.5	238	39.5	100.0	100.0	100.0	100.0
Buck Mountain Northern Ridge Top							
Chestnut Oak	350.0	100	28.0	37.1	39.0	75.8	50.6
Red Maple	493.8	100	6.3	52.3	39.0	17.1	36.1
Black Birch	100.0	56	2.6	10.6	22.0	7.1	13.3
Totals	943.8	256	36.9	135.7	100.0	100.0	100.0

Particularly striking is the uniqueness of the species compositions of the bottomland versus the northern ridge top. Hemlock and yellow birch almost equally dominate the bottomland to the exclusion of other tree species whereas on the northern ridge top, chestnut oak, red maple, and black birch dominate but neither hemlock nor yellow birch are present.

The shrub layer is not particularly well developed but does contain considerable hobblebush (*Viburnum alnifolium*) and some rhododendron (*Rhododendron maximum*). The herbaceous layer contains abundant woodferns (*Dryopteris* spp.), painted trillium (*Trillium undulatum*), wild lily-of-the-valley (*Maianthemum canadense*), sweet white violet (*Viola blanda*), and others.

Birds are not particularly visible in this forest owing to the dense canopy and its height. However, several noteworthy birds can be heard in the old-growth forest over the babbling of Swift Run. These include the winter wren, solitary vireo, black-throated green warbler, Louisiana water thrush, as well as the more common blue jay, ovenbird, black-capped chickadee, hairy woodpecker, slate-colored junco, and eastern phoebe.

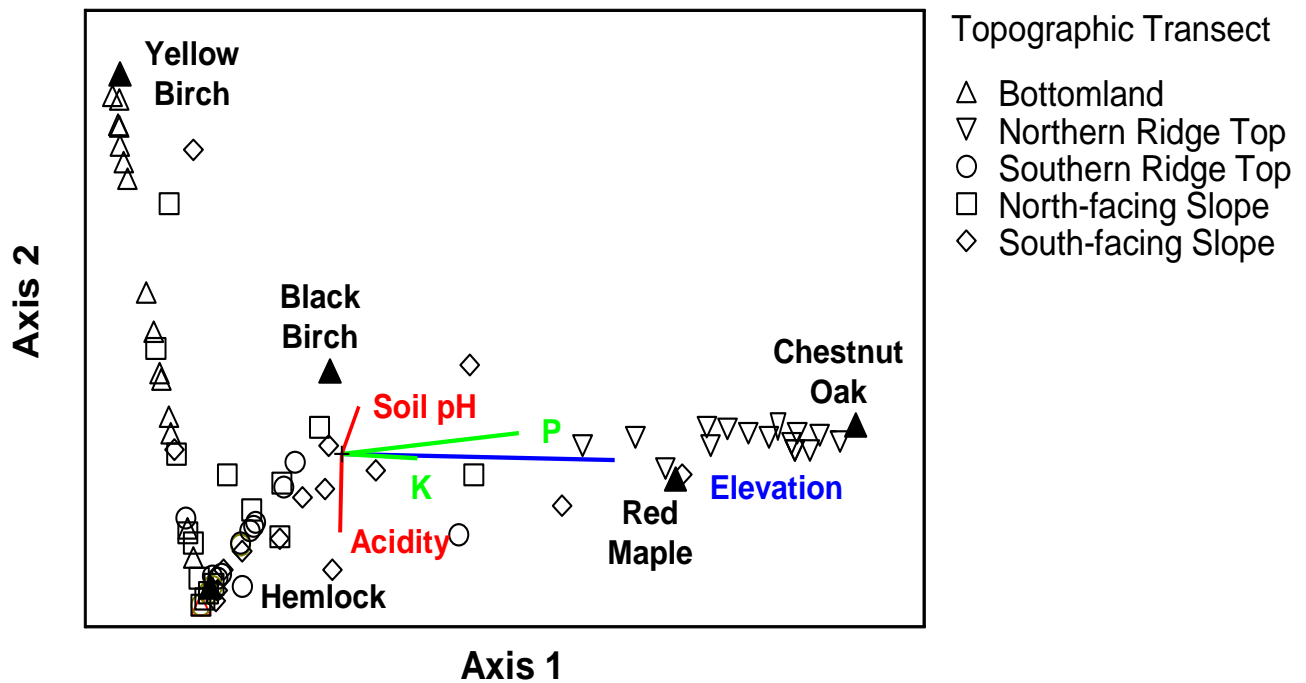


Figure 1. Detrended Correspondence Analysis ordination based on woody stems > 6 cm dbh sampled at the Snyder-Middleswarth Natural Area excluding eastern white pine and striped maple. The plot illustrates the distributions of the 80 sampled quadrats and five tree species on axes 1 and 2 with an overlay of vectors for significant correlates with the first two axes. The vector direction indicates the path of the gradient and its length, the strength of the correlation (Zawadzka and Abrahamson 2003).

Vegetative Patterns

Zawadzka and Abrahamson's (2003) ordination of species occurrences across the Snyder-Middleswarth Natural Area confirms the expectation that each tree species occupies its

own niche as indicated by their unique positions along the ordination axes (Figure 1). Axis 1 was correlated with a vegetation gradient from the chestnut oak and red maple on the northern ridge top to the hemlock/yellow birch bottomland. Axis 2 was correlated with the separation of the two birch species from hemlock. Axis 3 was associated with the separation of chestnut oak and red maple.

Several of the environmental and edaphic variables correlate with the axes of the ordination (Figure 1). For example, the phosphorus and potassium concentrations correlate with axis 1 ($r = 0.70$ and 0.46 , respectively), the axis related to the shift from hemlock and yellow birch to chestnut oak and red maple. Elevation was another correlate of axis 1 ($\tau = 0.54$). Thus, chestnut oak and red maple had greater dominance on soils with higher concentrations of phosphorous and potassium and at higher elevations than did hemlock or yellow birch. The correlation of hemlock with more acidic soils has been documented elsewhere (Woods 2000a) as has the association of yellow birch with less acidic soil (Erdmann 1990). Soil pH and acidity correlated ($r = 0.34$ and -0.44 , respectively) with axis 2, the axis related to the separation hemlock from both birch species. Thus, yellow and black birch are more dominant on soils with higher pH and hence, lower acidity than those where hemlock is predominant.

Size Distributions

Although no tree ages have been determined in the old-growth portion of the Snyder-Middleswarth Natural Area, Edward R. Cook (unpublished data) has cored eastern hemlocks in the nearby Bear Run area. Table 2 shows the results of the oldest dating of multiple cores taken from 12 hemlocks. The ages spanned 1641 to 1770 with many of these old hemlocks being relatively small (larger trees often have heart-rot and are thus hollow). Apparently, individual trees

Table 2. Ages of hemlocks determined by coring. Unpublished data furnished by Edward R. Cook, Tree-Ring Laboratory, Lamont-Doherty Geological Observatory of Columbia University, Palisades, NY 10964.

Site	Oldest Dating	Age in 1983 (years)	Site	Oldest Dating	Age in 1983 (years)
Bear Run	1641	342	Alan Seeger	1609	374
	1644	339		1611	372
	1651	332		1612	371
	1682	301		1616	367
	1712	271		1622	361
	1738	245		1640	343
	1738	245		1641	342
	1740	243		1649	344
	1743	240		1658	325
	1760	223		1667	316
	1765	218		1668	315
	1770	213		1684	299

can spend long periods of time in a suppressed condition. When a large canopy-dominating hemlock falls within the immediate vicinity of a suppressed tree, it presumably grows rapidly to fill the canopy gap.

Although tree-size data do not accurately represent tree ages, such data can provide insight into the successional status of tree species. The following graphic models, for example, illustrate the expected size-class distributions for hypothetical species with stable, successfully invading, unsuccessfully invading, and senile size-class structures (Figure 2). Actual size-class data can be compared to these expectations to understand the history and future success of a each species in a given forest stand.

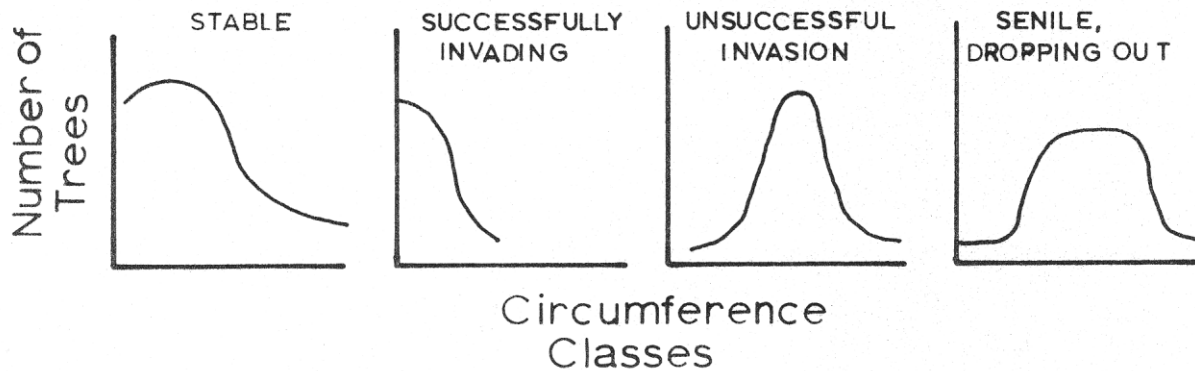


Figure 2. Graphic models expressing the theoretical size structure of tree species that have stable, successfully invading, unsuccessfully invading, and senile size-distribution structures.

The huge cathedral-like towers formed by the hemlocks of the Snyder-Middleswarth old-growth forest are impressive. Although the large hemlocks dominate the scene, there are, however, far more young hemlocks than old. Given the theoretical expectation illustrated in Figure 2, we would expect that species like hemlock should show a frequency distribution of tree ages or tree sizes that has positive skewness (skewed right), indicating a stable population. Zawadzka and Abrahamson (2003) provide diameter size-class histograms for hemlock, yellow birch, chestnut oak, and black birch (Figure 3). Hemlock's size-class distribution suggests a stable distribution and indicates that hemlock is replacing itself within the community. The size-class histogram for yellow birch implies that substantial losses are occurring from the smallest to the second smallest size class, nevertheless the distribution is indicative of a population that is replacing itself. The histogram for chestnut oak suggests that either the establishment of chestnut oak or its recruitment to larger size classes has been hindered in recent decades. Although numerous individuals were sampled in the smallest size class, few individuals were sampled in the subsequent size class. The size-class histogram for black birch suggests episodic recruitment, implying that natural disturbance such as wind storms may affect its recruitment. There were very few large individuals of black birch likely because of its short longevity compared to hemlock and yellow birch.

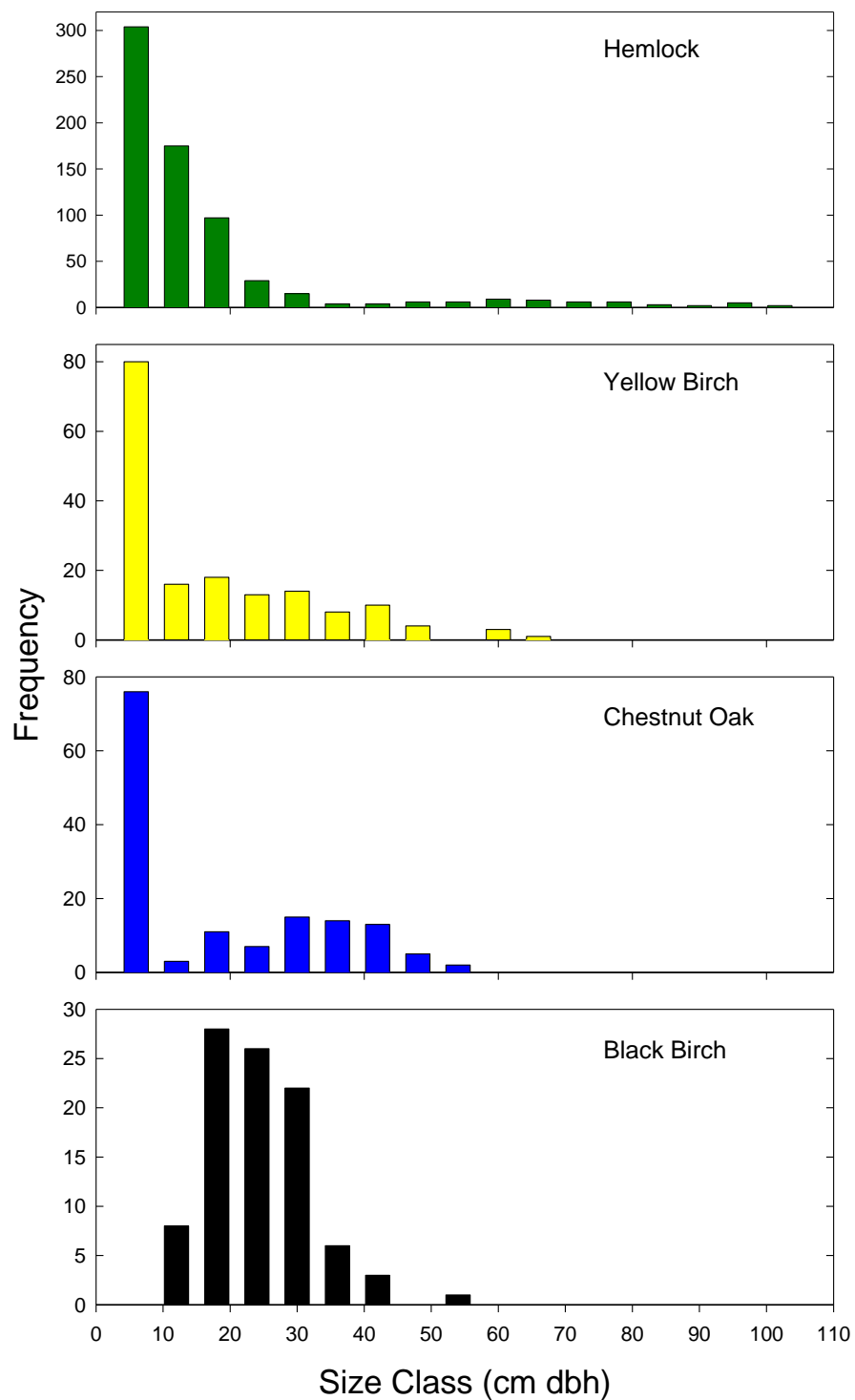


Figure 3. Size-class distribution for all eastern hemlock, yellow birch, chestnut oak, and black birch stems sampled at the Snyder-Middleswarth Natural Area (Zawadzkas and Abrahamson 2003).

The Future of This Old-growth Forest

Hemlock is the most shade tolerant (Whitney 1990) of those species present in the Snyder-Middleswarth forest and hemlock's dense canopy can have inhibitory effects on the regeneration of other species including yellow birch (Woods 2000a). Hemlock's ability to regenerate under low resource conditions (e.g., low light and low soil pH) sets up a positive feedback that can favor hemlock over other species (Catovsky and Bazzaz 2000). The current stem-size distributions in this forest suggest that hemlock will continue to dominate the Snyder-Middleswarth landscape into the foreseeable future. However, disturbances including catastrophic blow downs, fire, and herbivory by exotic pests such as the hemlock woolly adelgid (*Adelges tsugae*) could reduce its future dominance enabling birch species, red maple, and even white pine to gain importance (Zawadzkas and Abrahamson 2003).

The ability of yellow birch to persist in hemlock-northern hardwood forests is dependent on episodic canopy disruption as yellow birch declines under a disturbance regime that creates only small gaps (Woods 2000a, b). Because of its relative shade intolerance, yellow birch has limited regeneration beneath dense hemlock canopies and hence, its regeneration occurs primarily in canopy gaps associated with nurse trees (Woods 1984, Runkle 1985, Catovsky and Bazzaz 2000). The persistence of yellow birch in the Snyder-Middleswarth forest may be due to the considerable canopy disturbance owing to frequent blow downs (Zawadzkas and Abrahamson 2003). Tip-up mounds and decaying down trees are common throughout the forest. Disturbance caused by high flows in Swift Run following large precipitation events may also contribute to the regeneration of yellow birch in the bottomland as large hemlock have occasionally been undercut by the erosive action of Swift Run (Zawadzkas and Abrahamson 2003).

Red maple and chestnut oak dominance increases with elevation on the south-facing slope and both species reach substantial density and dominance on the northern ridge top. Red maple exhibits characteristics of both early and late successional trees in that it can persist in late-successional forests but it can increase markedly following a wide range of disturbances (Lorimer et al. 1994, Abrams 1998, Orwig and Abrams 1999) including wind throws which are the primary source of canopy gaps in the Snyder-Middleswarth forest (Abrahamson, personal observation). Furthermore, the steepness (mean = 52%) of the south-facing slope and its southern exposure may generate sufficient disturbance (e.g., down-slope rock and/or soil movement, periodic xeric conditions limiting juvenile survival) to encourage opportunists like red maple and chestnut oak. Chestnut oak is typically associated with dry, well-drained, and often low-nutrient soils (Elias 1980, Greller 1988) and it responds favorably to disturbance (Nowacki and Abrams 1994). However, the stem-size distributions of chestnut oak suggest that it has not consistently recruited new individuals into its population (Zawadzkas and Abrahamson 2003). The shortage of smaller-sized individuals could be a consequence of episodic recruitment, periodic bouts of high mortality due to drought or other catastrophic events, or juvenile mortality due to deer browsing or insect herbivory including that of gypsy moths.

Black birch was the second most frequent species and it was particularly abundant on the north-facing slope and the southern ridge top and absent only in the bottomland. Perhaps because of this wide and abundant distribution, black birch occurrence had only a weak correlation with axis 2, the axis correlated with soil acidity. Alternatively, this general lack of correlation may be a consequence of black birch being dependent on episodic recruitment as an opportunistic invader of gaps. Within the Snyder-Middleswarth forest, relatively frequent blow downs cause marked local increases in light and possibly other resources. Black birch is strongly responsive to increased light whereas the dominant hemlock exhibits small changes in juvenile survival and growth under elevated light conditions (Catovsky and Bazzaz 2000).

The infrequent occurrence of white pine at the Snyder-Middleswarth Natural Area contradicts references to this forest as a hemlock-white pine forest (Erdman and Wiegman 1974, Pennsylvania Bureau of Forestry). It is possible that white pine was once more abundant given that it is an early to mid-successional species that only recruits into old-growth forests following major disturbances (Abrams and Orwig 1996, Orwig and Abrams 1999). Medium to large-sized canopy gaps are required for its recruitment and some (Foster 1988, Rooney 1995) have suggested that a combination of wind throws and fire may be necessary for successful establishment. Thus, white pine can exist as a gap-phase species (Abrams et al. 1995) but substantial recruitment is dependent on larger-scale disturbances (Abrams and Orwig 1996, Abrams et al. 2000).

Even though elevation was a principal correlate of the vegetation gradient from the bottomland to the northern ridge-top community, it is unlikely that an absolute elevation difference of < 330 ft, in and of itself, is the cause of this acute change in species dominance. Rather, the elevation gradient is likely a reflection of the interactions of other gradients including the phosphorus and potassium concentration gradient that the Zawadzka and Abrahamson (2003) analysis found and other unmeasured gradient such as soil moisture, water drainage, or occurrence of wind throws.

The increase of phosphorus and potassium from the bottomlands to ridge tops recorded in the Zawadzka and Abrahamson (2003) study is the reverse of the more usual pattern of having richer colluvial aprons in the valleys within the Pennsylvania Ridge and Valley Province (Eckenrode 1985). We can hypothesize that the pattern recorded is a consequence of Swift Run's bottomlands being scoured back to bedrock by late Pleistocene erosion while the ridge crests were less disturbed and hence remained richer (Ben Marsh, personal communication). Detailed assessments of the valley's soils have yet to be performed.

The Snyder-Middleswarth Natural Area exhibits the expected characteristics of a well-developed old-growth forest, e.g., tree ages exceeding 300 yr (ages determined from fallen log sections), low tree densities distributed among all size classes, trees with diameters > 70 cm, and volumes of dead wood (Spies and Franklin 1988, Tyrrell and Crow 1994). Consequently, we would expect that the observed distributions of species reflect both the distributions of key environmental and edaphic influences as well as historic and current disturbance events. Furthermore, we might posit that competition among tree species would amplify the correlation of species occurrences with environmental and edaphic factors because competitive interactions should act to reduce the number of individuals persisting on microsites to which they are poorly adapted.

Threats to the Snyder-Middleswarth Natural Area

Acid precipitation has seriously impacted the area by enhancing the acidity of Swift Run. The water that enters Swift Run moves through Tuscarora sandstone, the hardest of the sandstones in our region. Tuscarora sandstone contains so little Ca that it is unable to buffer strongly acidic precipitation. The consequence is that the portion of Swift Run within the old-growth forest area has a pH too low for fish such as the native brook trout to survive (low pH releases aluminum, which in turn is toxic to fish and other aquatic organisms). The unnamed creek that joins Swift Run near the parking area has a substantially higher pH because its waters percolate through Juniata sandstone, which has greater buffering ability. As a result, fish such a brook trout do occur as far upstream as the confluence of these two creeks.

The continued domination of the Snyder-Middleswarth old-growth forest by hemlock could be appreciably impacted by an outbreak of the hemlock woolly adelgid. This exotic herbivore was first reported in southeastern Pennsylvania in the late 1960s (McClure 1987) and it has been observed in this old-growth forest since 2003 (Abrahamson personal observation). Should appreciable hemlock mortality occur due to adelgid damage, black birch would likely gain

considerable importance (Orwig et al. 1998). Other herbivores including the elongate hemlock scale, spruce spider mite, hemlock rust mite, and cryptomeria scale could also threaten hemlock survival at the Snyder-Middleswarth Natural Area.

White-tail deer browsing, currently among the most important agents of forest disturbance in the eastern United States, is a third threat to the old-growth forest. In Pennsylvania over browsing dates to the 1930s and its impacts are evident even in old-growth areas such as the hemlock-white pine-northern hardwoods at Heart's Content (Whitney 1984, Rooney and Dress 1997). Such browsing can shift the balance of canopy species because of differential recruitment by less-preferred and often light-requiring species such as red maple, black birch, and yellow birch (Whitney 1984, 1990; Rooney 1995; Abrams et al. 2000, 2001). There is evidence of deer use (droppings) and browse within the Snyder-Middleswarth old-growth forest. The gap in the smaller size classes of chestnut oak may be a consequence of juvenile mortality due to deer browsing. However, Zawadzka and Abrahamson (2003) did not see the same gap in smaller size classes with hemlock, a species that can be used as winter browse by deer in areas with high deer densities (Anderson and Loucks 1979). On the other hand, small hemlock stems only a few cm in diameter can be more than a century old (M.D. Abrams personal communication). Consequently, even though small individuals of hemlock are present, it is possible that there has been limited hemlock recruitment for several decades.

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