

Chapter 4

Biodiversity in the Herbaceous Layer and Salamanders in Appalachian Primary Forests

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The southern Appalachians are considered one of the centers of forest diversity in the United States. A person entering a moist, uncut, primary cove hardwood forest in the spring will encounter a spectacular show of vernal wildflowers. These extraordinary displays lure thousands of tourists to the southern Appalachians every year. The ground often appears to be carpeted in a tapestry of whites, blues, reds, and yellows. More discerning visitors may note the exceptional species diversity of these displays. Duffy and Meier (1992) described stands in primary cove hardwood forests where 10 to 14 different species of spring flora occur in each square meter. A single hectare may contain thousands of large-flowered trilliums (*Trillium grandiflorum*), wake robins (*Trillium erectum*), yellow trilliums (*Trillium luteum*), Vasey's trilliums (*Trillium vaseyi*), Dutchman's breeches (*Dicentra cucullaria*), spring beauties (*Claytonia caroliniana*), trout lilies (*Erythronium americanum*), hepaticas (*Hepatica acutiloba*), windflowers (*Thalictrum thalictroides*), and larkspurs (*Delphinium tricorne*).

If visitors look closer still, particularly in the evening, they may observe salamanders, the most abundant vertebrate denizens of this region (Hairston 1987). Petranka, Eldridge, and Haley (1993) report that salamanders typically number one to two individuals per square meter. Meier and Bratton (in press) found six species in a single 25 x 25 meter plot, including the brilliantly striped Yonahlossee salamander (*Plethodon yonahlossee*), the southern redback salamander (*Plethodon serratus*), and the salamander-eating Blue Ridge Spring salamander (*Gyrinophilus porphyriticus danieli*).

Both salamanders and vernal wildflowers are groups of organisms that attain exceptional abundance and diversity in the southern Appalachians. Therefore, the response of these groups to forest management in this region is particularly important for both local and global biodiversity. Vernal herbs and salamanders share a set of characteristics including dependence on moist environments, long generation times, low reproductive rates, slow dispersal, and an association with mortality of mature canopy trees that cause them to show similar response to forest management.

Definitions

Duffy and Meier (1992) provide the definitions that we will use for primary, secondary, and mature forests: ". . . we use *primary* to describe forests that have never been clearcut and that have little or no evidence of past human activity. Such forests may have been grazed, they may have experienced limited exploitation of valuable tree species, and their floors may have been burned by Amerinds and European pioneers. Primary forests contain abundant downed timber in varying states of decay, standing dead trees, and live trees in a range of sizes. *Secondary* forests are those that have developed after the previous forest was extensively logged or clearcut. We use *mature* to refer to secondary forests that have existed longer than the normal harvesting rotation practiced by foresters on that particular forest type."

History

Why are there only a few remnants of primary forest left in the southern Appalachians? Native Americans began clearing parts of the forests perhaps 12,000 years ago (Dickens 1976). Native American settlement appears to have been concentrated in the floodplains and had little permanent effect. Settlement by Euro-Americans began in the 18th century and increased the extent and permanence of forest clearing (Lambert 1958). Timber harvesting for industrial purposes logged much of the forests of the southern Appalachians between 1880 and 1920 (Frothingham 1931). Catastrophic fires frequently followed the logging (Ayres and Ashe 1905). In 1911, the Weeks Act authorized federal purchase of forests for the protection of watersheds. Today, approximately two-thirds of the region is forested, with one-fifth of this land managed as national forests (Boone and Aplet 1994). In excess of 500,000 additional forested acres are within Great Smoky Mountains National Park.

How much primary growth is left in the southern Appalachians? Most of the forests in the region are even-aged and less than 100 years old. However, the

southern Appalachians contain one of the largest concentrations of primary forests east of the Mississippi River (Davis 1993). Stands that are 100 years or older constitute approximately 480,000 acres of the 11.3 million acres of timber-base land in the southern Appalachian region of Virginia, Georgia, North Carolina, and South Carolina (Boone and Aplet 1994). Doubtless this number will be adjusted as the Forest Service data on which this survey was based are improved. These 100-plus-year stands are considered potentially as primary, though many may prove to be older secondary forests or simply misidentified. An additional 100,000 acres of forests considered to be high in primary attributes exist within the boundaries of Great Smoky Mountains National Park (Houk 1993). The vast majority of old-growth acreage appears to lie within the federal lands (Boone and Aplet 1994).

The southern Appalachians are a region of exceptional plant diversity for the temperate zone. Well over 2,000 species of native vascular plants are known from this region. One of the more conspicuous components of southern Appalachian forests, especially mesic sites, is the vernal herbaceous community (Braun 1950). The southern Appalachians are also considered the center of salamander diversity on earth (Petranka, Eldridge, and Haley 1993). Boone and Aplet (1994) report 54 species of salamanders in the region. Salamanders comprise the largest portion of the vertebrate predator biomass of these forests (Hairston 1987).

Primary Forests Vs. Secondary Forests

Prior to European settlement, the landscape of the region was dominated by forests (Bartram 1792). Pickett and White (1985) note that anthropogenic disturbance in the form of agriculture and logging have interrupted the gap dynamics of the forest and led to the creation of uniform stands of successional overstories above understories dominated by shade-tolerant species.

Perhaps a short description of the disturbance regime will help clarify the conditions under which most of these species have survived since the Pleistocene. This regime is important because disturbances help regulate the composition, structure, and function of forests (Pickett and White 1985). Fire in the primary cove hardwoods of the southern Appalachians appears to be infrequent. Harmon, Bratton, and White (1983) found an historic fire-return frequency for Great Smoky Mountains National Park as a whole of 840 years for human-caused fires and 30,000 years for lightning-caused fires. Fires of both types are extremely rare above 1,000 meters (Harmon, Bratton, and White 1983). Goodwin (1977) suggests that Native Americans frequently set fires prior to Euro-American settlement. Euro-Americans often burned sub-mesic and relatively xeric forests below 1,500 m (Ayres and Ashe 1905). Lorimer (1976) found no evidence of fire in trees that he cored in the Poplar Grove of

Joyce Kilmer Memorial Forest during the past 300 years; furthermore, he found no evidence of charcoal in the upper layers of soil. Wind disturbance probably plays a greater role than fire. Lorimer suggests that blowdowns may have eliminated as much as 15% of the canopy within the Poplar Grove during a few peak disturbance decades.

Gap formation resulting from tree falls is the most common natural form of canopy disturbance in moist primary forests (Runkle 1982). Runkle (1981, 1982) examined gap size and frequency in a number of primary mesic forest stands in the southern Appalachians, including stands in Great Smoky Mountains National Park, Joyce Kilmer, and Walker Cove. Gap size ranged from 1 to 1,490 square meters, with a geometric mean of 65 square meters. New gaps formed at an average rate of 1% of land surface area per year. As a result of the disturbance, primary Eastern forests usually have irregular all-age structures (Lorimer 1976).

It is important to understand the influences of the present even-aged management on the diverse flora and fauna, including salamanders, of the southern Appalachians—for three reasons. First, much of the forested landscape there is now occupied by even-aged second growth. Second, current forest management plans include further fragmentation and additional harvests leading to even-aged stands even on some of the forest currently identified as old growth. Finally, it is assumed by many that maturing secondary forests will adequately replace primary stands. This chapter challenges the validity of this last assumption.

The scientific literature includes several studies attempting to detect recovery of forest understories following major disturbance. In hardwood stands in New Brunswick, Canada, MacLean and Wein (1977) found little evidence of recovery of late-successional herbaceous species several decades after canopy opening. Flaccus (1959) found that, following landslides in the White Mountains of New Hampshire, 72-year-old herb communities were similar to older (200+ years) forests, but a number of primary species were still absent from the 72-year site. Brewer (1980), working in old growth in Michigan, concluded that the herbaceous community was still recovering from a major disturbance event 150 years prior. Studies in Great Britain indicate that recovery of forest herbs after an area has been used for agriculture may take centuries (Peterken and Game 1984). Bratton and Miller (1994) found that understory plants on Cumberland Island, Georgia, were severely reduced following agricultural disturbance even after a century, though the overstories had appeared to recover. Similarly, salamanders suffer profound and long-term negative effects after logging. These effects have been observed both in the Pacific Northwest (Bury 1983 and Welsh 1990) and in the Eastern U.S. (Bennett, Gibbons, and Glanville 1980; Raymond and Hardy 1991).

Vernal herbaceous richness in one-square-meter plots was consistently

higher in primary cove hardwood forests in the southern Appalachian Mountains than in comparable secondary forests (Duffy and Meier 1992; Meier, Bratton, and Duffy, in press). In 10 paired primary and secondary sites, species richness in 1 m² quadrants averaged 11.2 species on primary sites and 6.9 on secondary sites. We found no evidence that cover or richness of vernal herbs recovers even after almost nine decades (Duffy and Meier 1992). This suggests three possibilities: (1) that recovery is so slow or variable among sites that 90 years is insufficient time to detect it; (2) that such forests will never recover to match remnant primary forests, because they have reached an alternative lower diversity state, perhaps because climatic conditions are different today than when the forests became established; or (3) that herbaceous plants depend on gap-phase dynamics caused by the death of trees, so that recovery must await the growth, death, and decomposition of the trees of the secondary forest. Whatever the mechanism, herbaceous understory communities in the mixed-mesophytic forests of the Appalachians appear unlikely to recover within the present planned logging cycles of 40 to 150 years, suggesting continuing loss of diversity of understory herbaceous plants.

We have found no species of vernal herbs that are only in primary forests; however, many species occur more frequently in primary forests and a few of these occur much more frequently there. We have not found any of these to be ubiquitous across all southern Appalachian primary forests. Species that appear much more frequently in primary forests include dwarf ginseng (*Panax trifolium*) and *Cynophyllus fraserianus* in Great Smoky Mountains National Park, and Goldie's woodfern (*Dryopteris goldiana*) in the Toecane District of Pisgah National Forest.

We would like to suggest the existence of five ecological mechanisms for reducing or limiting species richness per plot (alpha diversity) of vernal herbs and salamanders in logged stands, three of which may also account for the slow recovery of some species: (1) Logging directly reduces populations of salamanders and rarer herbs; (2) populations of forest-floor species are further reduced during the successional stages following logging, either by inability to adapt to changed microclimate or, in the case of herbs, by competition with r-selected species ("weedy" species with high reproductive and dispersal rates), which are better dispersers and better able to tolerate desiccation and increased radiation; (3) forest-floor herbs have slow growth and both these herbs and salamanders have low reproduction rates, thus population densities increase slowly; (4) many forest-floor herbs and salamanders are slow dispersers, thus they are slow to reoccupy suitable habitat once locally extirpated or greatly reduced in population numbers; and (5) secondary forests may have less than optimal conditions for forest-floor herbs and salamanders because microhabitats on the forest floor, including well-decayed large logs and gaps, may be temporarily eliminated by interruption of gap-phase dynamics.

Mechanism 1: Logging-Caused Diversity Loss

Disturbance that accompanies logging negatively impacts salamanders and vernal herbs. The harvesting systems and the occurrence of associated disturbances, such as burial under slash, will determine the degree to which the forest-floor flora and salamanders are affected.

The results from even a small recent clearcut demonstrate early loss of vernal herbs (Meier, Bratton, and Duffy, in press). We find an initial loss of vernal herbs soon after clearcutting followed by a lack of recovery, if not continuing losses of vernal herbs through age 87 (Duffy and Meier 1992). This agrees with the temporal sequence of vernal herb diversity after the logging of second-growth stands predicted by Bormann and Likens (1979). However, unlike Bormann and Likens's prediction, we find that diversity of vernal herbs is higher in primary forest than in recently clearcut stands (Duffy and Meier 1992). Petranka, Eldridge, and Haley (1993) examined clearcut stands 10 years or less old and concluded that salamander abundance was reduced by 75% or more following clearcutting, and species per plot were reduced by about half.

Petranka, Brannon, and Hopey (in press) examined the influences of intensive timber management on southern Appalachian salamander communities. Their comparison of clearcuts with mature forests led them to conclude that clearcuts almost completely eliminate terrestrial salamander populations. Aquatic and semi-aquatic salamanders were also severely reduced in abundance. They conclude that more than 120 years may be required for salamander populations to recover after disturbance. Meier and Bratton (in press) obtained similar results, finding a correlation between stand age and both number of salamander species detected per plot and number of salamander individuals detected per plot. The highest number of species per plot was found in the one primary stand that they examined.

Mechanism 2: Stress, Competition, and Herbivory

Even if logging is carefully conducted and few herb populations are damaged in the process, removal of trees still opens the forest canopy and initiates succession. In the Eastern United States, "high-grading" (the removal of a few exceptionally valuable trees) or careful selective cutting may have effects similar to gap-phase succession (Meier, Bratton, and Duffy, in press). However, clearcutting may allow more disturbance-tolerant genera to increase in frequency and cover, displacing populations of less disturbance-tolerant forest-floor herbs.

Community organization for spring ephemerals in relatively undisturbed forest is based on a mixture of biotic and abiotic factors, including competition

for light, pollinators, and nutrients; species-specific microhabitat preferences; canopy species; and stand history (e.g., Bratton 1976; Muller 1978; Hicks 1980; Motten, Campbell, and Alexander 1981; Givnish 1982; Beatty 1984; Rogers 1985; and Motten 1986). Together these studies suggest that vernal species may be eliminated by competition for light and nutrients from taller herbs and shrubs. Further, some vernal herbs occupy very specific types of microhabitats on the forest floor, and once displaced may not be able to survive on other, less suitable sites.

Following clearcutting in a watershed in the southern Appalachians, moisture contents of the O horizons of the soil were reduced by as much as half; however, moisture in the A horizon increased (Swank and Vose 1988). Perhaps more detrimental, mean monthly surface temperature was elevated by as much as 10° C. Daily maximum temperatures sometimes exceeded 54° C in summer. Such temperatures can be hazardous to both herbs and salamanders. Ash (1988) found an increase in bare soil in clearcuts, and Raphael (1988) found a decrease of litter in clearcuts. Loss of litter may expose shallow roots, desiccate vernal herbs, and decrease cover for salamanders. Many forest herbs are not adapted to making photosynthetic use of the greater light availability that results from the removal of the canopy (Hicks and Chabot 1985). Increased temperatures in summer lead to increased metabolic cost. Many vernal herbs lack the ability to sustain such cost and may experience mortality or reproductive failure (Nault and Gagnon 1993). Petranka, Eldridge, and Haley (1993), Petranka, Brannon, and Hopey (in press), and Spotila (1972) point out that most salamanders require moist environments to avoid desiccation. Petranka, Eldridge, and Haley (1993) also point out the sensitivity of southern Appalachian salamanders to increases in soil surface temperature following intensive logging.

In the Susquehanna River gorge, Bratton, Hapeman, and Mast (1994) found that on 25 x 50 meter plots, early successional old fields had fewer vernal herb species than did stands with pole-sized trees. These in turn had fewer species than mid-successional stands, which had fewer species than mature stands. The low frequencies of species such as northern nodding trillium (*Trillium flexipes*) and squirrel corn (*Dicentra canadensis*) in the pole-sized stands also indicate that some herbaceous species have been nearly extirpated, either by the disturbance that opened the canopies or by subsequent successional processes. It is important to recognize that some herb species occur much less frequently in younger stands than do others, and that the ecological tolerances of the herbs may contribute to this.

Open successional sites and the initial stages of forest regrowth may also be more prone to browsing by white-tailed deer (*Odocoileus virginianus*) (Collam and Curtis 1956; Alverson, Waller, and Solheim 1988; Meier, Bratton, and Duffy, in press). This problem may become more severe with increasing forest fragmentation and white-tailed deer populations.

Mechanism 3: Low Reproduction Rates and Slow Growth

A third reason that vernal herb diversity and abundance may remain low, even decades after logging, is that herbaceous plants of late-successional forests mature slowly—some species of vernal herbs take a decade or more from seed to first flowering (Curtis 1943, Bierzychudek 1982a). Likewise, Hairston (1983) and Hairston et al. (1992) indicate that many salamanders have long generation times, and Petranka, Brannon, and Hopey (in press) suggest that long generation times may slow salamander recovery in secondary forests. Upon reaching maturity, many vernal herb species produce few seeds. Many species also demonstrate slow rates of growth. Growth as little as 1 cm yr⁻¹ has been reported from a wide variety of late-successional forest herbs at sites in the northern United States and Canada (Sobey and Barkhouse 1977, Whitford 1951). Meier, Bratton, and Duffy (in press) suggest that growth rates in the South are similar to or slower than northern rates, rather than faster. Second, slow vegetative growth of late-successional herbs may reflect a K-strategy of restrained investment in reproduction and growth (Gadgil and Solbrig 1972, Bierzychudek 1982a) and increased allocation of resources to energy and nutrient storage (Newell and Tramer 1978) in an environment where competition is severe for soil nutrients (Rogers 1985) or for light (Givnish 1982). Such competition may be more a factor of successional state than of latitude; but studies of northern old growth have not been undertaken.

Given a time lag of up to a decade from seed to first flowering for many vernal species and limited seed production of late-successional understory herbaceous plants, slow vegetative growth should contribute to slow recovery following logging. Meier, Bratton, and Duffy (in press) found that for large-flowered trillium, wake robin, and yellow trillium, populations in secondary forest, where they occurred, were significantly lower in density than populations in primary forest. This suggests that slow population growth is a factor leading to low densities of trillium in secondary forests.

Mechanism 4: Limited Spread and Slow Dispersal

Understory herbaceous plants exhibit a variety of life-history strategies, but many are functionally clonal (Whitford 1949, Harper 1977) and long-lived (Whitford 1951, Cook 1983). Clonal species may be slow to reoccupy large areas. Whitford (1949) found that some herbaceous species became more evenly distributed in later successional stages. He suggested, without direct measurement, that patches of such species are larger in late succession. He suggested that reproductive strategies determined spatial distribution: Clonally reproducing species became less patchy with apparent increases in stand

age, whereas species with widely dispersed seeds showed no change in distribution. Primary sites appear to contain networks of overlapping clonal patches of different species (cf. Whitford 1949). Parts of patches may die or be displaced by other species so that remnants of the original clones become noncontiguous. Recolonization of disturbed sites is likely to be slow because late-successional herbaceous species tend to spread by clonal growth or by gravity- or ant-dispersed seeds (Beattie and Culver 1981), limiting the rate at which deforested areas can be colonized. In addition, single species of ants may be the sole agents of seed dispersal for some species (Don Waller, University of Wisconsin, Madison). Matlack (in press) has reported that rates of seed dispersal can be extremely slow. For example, he found that the rate of dispersal of black cohosh (*Cimicifuga racemosa*) was effectively zero meters per year.

Other species of vernal herbs are dispersed by gravity—for example, dwarf ginseng (Philbrick 1983). Meier, Bratton, and Duffy (in press) found that dwarf ginseng dispersed its seeds within 25 centimeters of the mother. Given the slow rates of dispersal and the short distances that propagules are dispersed from parent plants, landscape features such as high elevations, dry ridges, roads, and agricultural fields may present impassable barriers to dispersal for these plants.

Petranka, Brannon, and Hopey (in press) and Meier and Bratton (in press) suggest that the slow recovery of salamander populations can be explained in part by extremely slow dispersal of salamanders (Hairston 1983, Hairston et al. 1992). Meier and Bratton (in press) found that forest fragments of less than 10 hectares were depauperate of salamanders and suggest that forest fragmentation may present nearly insurmountable barriers to recolonization of severely disturbed sites.

Mechanism 5: Habitat Loss and Disruption of Gap-Phase Succession

Differences in physical structure and cover between primary and second-growth understory herbaceous communities may affect the functioning of forest ecosystems. Braiton (1976) found that some species of vernal herbs most commonly root in deep pockets of organic matter or at the base of trees or on fallen logs. Therefore, removal of organic materials, especially logs, may reduce microhabitat availability for vernal herbs. Petranka, Brannon, and Hopey (in press) and Meier and Bratton (in press) found correlations between the number of individual salamanders and salamander species per plot and the availability of well-decayed coarse woody debris. Petranka, Eldridge, and Haley (1993) found a positive correlation between such coarse woody debris and forest maturity.

Logging also modifies the distribution of light on the forest floor. Clearcuts change from intense light to very limited light as succession closes the canopy. Canopy gaps are infrequent in younger successional forests and probably continue to decline in the Appalachians until at least age 80. It may require 150 to 200 years before gap-phase processes are completely reestablished. Tree falls produce not only pits and mounds and fallen logs that provide new microhabitats, but also small areas of elevated but not extreme radiation. Because canopy gaps are partially shaded, they are not as desiccating as open clearcuts, nor are they as likely to be invaded by r-selected species or exotics.

Meier, Bratton, and Duffy (in press) found that *Cimicifuga americana* was more abundant in canopy gaps and that its fruiting was significantly dependent on and positively associated with the presence of gaps. Thus, the reduced gap formation in secondary forests may lead to a lack of recovery or even decline in *C. americana* populations, a phenomenon that may also apply to other gap-dependent species. Moore and Vankat (1986) found that herb cover slowly increased within gaps.

Management Implications

Meier, Bratton, and Duffy (in press) found no correlation between size of primary stand and mean number of species per square meter. This result suggests that even small remnant primary forest stands are important reserves of vernal herb diversity. Nevertheless, while preservation of small tracts of primary forest appears to be important in maintaining diversity, they may not be adequate to preserve diversity on regional and larger scales. Vernal herbs and salamanders would be slow to recolonize clearcut areas from small remnant primary stands because of slow growth, low rates of reproduction, poor dispersal, loss of suitable habitat, and disruption of gap-phase dynamics. The caveat for forest management is that larger remaining blocks of primary forest should be protected as well as small stands; if only small tracts were left, one could expect a reduction in regional and global diversity.

Because vernal herbs and salamanders demonstrate low rates of recovery (Duffy and Meier 1992; Petranka, Eldridge, and Haley 1993), harvest methods that cause less mortality are preferable; for example, logging methods that mimic natural gap-phase dynamics may be less damaging than clearcutting. Because of the poor dispersal characteristics of many vernal herbs and salamanders, further forest fragmentation caused by the building of logging roads may pose additional barriers to recovery of these organisms. It is also possible that transplantation and active reintroduction of these species may help restore vernal herb and salamander populations of secondary mixed mesophytic forests.

Summary

Though the ecological effects of a clearcut are influenced by many things, such as the extent and shape of the cut, land contours, and the nature of the surrounding uncut forest, certain general trends can be expected. With canopy removal, nutrients are lost from the ecosystem. Logging equipment inflicts damage on both soil and herbs.

With the canopy removed, temperatures at the soil surface become greatly elevated during the summer, causing mortality of salamanders and shallow-rooted vernal herbs. Many forest herbs cannot make use of the greater light availability that results from canopy removal. When summer comes, increased temperatures lead to vastly increased metabolic cost, which many vernal herbs cannot afford because they are not very photosynthetically active during the hottest portion of the year. Many long-lived perennial herbs show slow population growth rates (Bierzchudek 1982b, Meagher 1982, Kinoshita 1987, Charon and Gagnon 1991, Nault and Gagnon 1993).

A closed-canopy stand begins to develop after about 15 years. This presents an additional problem for herbs that depend upon gaps for reproduction. This shortage of canopy gaps often continues through stand-age 80, and the size and rate of canopy gap formation will not achieve the levels found in primary forests before age 150 to 200 (Bormann and Likens 1979).

Some species benefit from the formation of canopy gaps, pits and mounds, and rotting logs. Canopy gap formation increases light availability, soil moisture, and soil nutrient availability. Canopy gaps, unlike clearcuts, provide a gradient of light intensity increasing from the edge of the gap toward the center. Clearcutting leads to a decrease in both spatial and temporal heterogeneity of the environment within the stand.

By the time canopy gap formation has been reestablished to the levels found in primary forests, many species have been eliminated from the clearcuts. Most vernal species are not adapted for rapid dispersal. In the southern Appalachians, there are many topographic barriers to dispersal. Even if a species becomes established in an area, it is still likely to show low rates of clonal growth and sexual reproduction. Clearcutting of primary mixed mesophytic forests causes mortality of many vernal herbs. Life history characteristics of these species lead to very long recovery periods, if recovery occurs at all.

All of these factors combine to retard recovery of the herbaceous understory in southern Appalachian forests. The low to nonexistent recovery rates observed for vernal forest herbs suggest that a landscape of hypothetically restored old secondary forest may not serve to conserve and restore vernal herb populations. Management plans should include protection of remaining primary mixed mesophytic forests.

The southern Appalachians are a center of diversity for both salamanders and temperate herbaceous flora. The more mesic primary forests of this region

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