

Bob Marshall's forest reconstruction study: three centuries of ecological resilience to disturbance¹

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IRELAND, A. W. (Department of Earth and Environmental Science, Lehigh University, Bethlehem, PA 18015), B. J. MEW (Biology Department, Oberlin College, Oberlin, OH 44074), AND D. R. FOSTER (Harvard Forest, Harvard University, 324 North Main Street, Petersham, MA 01366). Bob Marshall's forest reconstruction study: three centuries of ecological resilience to disturbance. *J. Torrey Bot. Soc.* 135: 411–422. 2008.—In 1924, Bob Marshall and his Harvard University advisor Richard Fisher developed an integrated historical approach for forest reconstruction to address ecological questions and provide insights to forest management. Their approach utilized complementary methods and data: dendrochronology, diverse historical records (e.g., deeds, town and oral histories, and census and lumber mill records), and intensive field mapping and sampling of the site including stumps and uproot mounds, and forest composition and structure. Marshall applied this approach broadly to a 61-ha *Tsuga canadensis* (eastern hemlock)-*Pinus strobus* (eastern white pine) forest on sandy dry soils and intensively to a 0.15-ha sub-plot. He sought to test his hypothesis that pine and hemlock displayed compositional resilience to disturbance and to understand the life-history and growth characteristics of the two species that enabled co-dominance. Marshall concluded that, in contrast with the successional tendencies of white pine across New England's mesic uplands, pine and hemlock had dominated on these dry, sandy soils since at least the early 1700s and through multiple episodes of logging. Based on his interpretation of the contrasting growth rates and shade tolerance of these species, he developed a simple model of forest development and silviculture to guide management on dry sites for pine and hemlock timber production. Fisher, Marshall, and Harvard Forest colleagues used these historical insights to plan a suite of harvesting experiments on the site in 1924–25 to perpetuate hemlock and pine. Unfortunately, the hurricane of 1938 and subsequent salvage logging terminated the experiment. In 2007, we tested Marshall's interpretations and prediction of resilience in this forest by examining its long-term response to the series of intense disturbances. We synthesized decades of observations, photographs, and data, and relocated Marshall's plot to measure forest age and size structure, composition, and site features including decaying stumps, pits, mounds, and bent and sprouting individuals. The current hemlock and pine forest is strikingly similar in structure and composition to that of 1924. These results reinforce Marshall's conclusion that hemlock and white pine forests on well-drained sandy soils can be remarkably resilient in composition to intense disturbance. The work highlights the development and application of an integrated approach to forest reconstruction by Marshall and Fisher and underscores the contribution of historical insights to addressing basic ecological questions, designing large long-term field experiments, and guiding forest conservation and management.

Key words: ecological resilience, Richard Fisher, forest harvesting, forest reconstruction, Harvard Forest, hemlock, hurricane damage, land use history, long-term experiments, Bob Marshall, *Pinus strobus*, *Tsuga canadensis*, white pine.

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Resilience, the ability of an ecosystem to maintain or recover its structural, compositional or functional characteristics after disturbance, has become a focus of research as ecologists have recognized the prevalence of natural disturbances and the increase in perturbations and stresses wrought by human activity (cf., Holling 1973, Peterson et al. 1998). In recent decades, the concept has been expanded to encompass adaptive management

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of ecosystems in the face of disturbance and stress as well as the capacity of social systems to respond to and shape ecosystem dynamics in an informed manner (Gunderson and Folke 2005). Thus, the concept of resilience underlies much of the basic research and applied management that engages conservation biology and restoration ecology (Ives and Carpenter 2007).

Forest resilience, both the inherent ability of forests to recover from disturbance and the ability of managers to maintain or restore ecosystem characteristics, has been a long-standing concern for foresters seeking to develop reliable timber sources based on relatively stable forest composition and productivity through time (Fisher 1918, Spurr and Cline 1942, Raup 1964, Whitney 1993). The lengthy tradition of forestry studies, including historical research, large manipulative experiments, and opportunistic observational studies, provides considerable insights into the dynamics of forest composition and structure. It also yields important lessons regarding management in the face of disturbance and changing social conditions (Barnes et al. 1998).

Two prevailing perspectives on the compositional resilience of New England forests developed through research largely centered at the Harvard Forest. One view, which largely predominates today, emerged from the work of Hugh Raup, Harvard Forest director from 1946–1967. Based on extensive historical research and forest reconstructions by his students, Raup concluded that the region's forests of oaks (*Quercus*), maples (*Acer*), birches (*Betula*), ash (*Fraxinus*), hemlock (*Tsuga canadensis* L. Carr.), and white pine (*Pinus strobus* L.) displayed extraordinary resilience to human impacts (Raup 1957, 1964, 1981). He based these conclusions on two broad observations: 1) despite a lengthy history of land clearance, logging, grazing, burning, and other impacts, trees and forests return to most upland areas. Forests, as a structural vegetation type, are extremely resilient in this region. 2) Over a three-century period of human and natural disturbance, there has been little change in the relative abundance of major tree species in the landscape. Forests exhibit strong compositional resilience (Raup 1964; cf., Whitney and Foster 1988, Foster et al. 1997). Raup attributed the structural and compositional resilience of these forests to the adaptation of

tree species to millennia of natural disturbances including wind and ice storms, fire, pests, pathogens, climate change, and glaciations (Raup 1981).

While many scientists support Raup's general observations, at least two caveats have been raised. Paleocological and historical studies document that although the major tree species persisted over time there have been notable changes in their relative abundance since European settlement (cf., Fuller et al. 1998, Foster et al. 1998, Cogbill et al. 2002). Other studies also underscore that while Raup's statements may hold for the region, at a stand and landscape scale many forests have been compositionally dynamic (cf., Henry and Swan 1974, Foster and Zebryk 1993).

One of the first people to examine this issue of stand-level resilience was Raup's predecessor, Richard Fisher (Harvard Forest director 1907–34). Studying stands of white pine, one of the most common and economically important trees in the early 20th century landscape of New England, Fisher concluded that the forests were successional and lacked compositional resilience (Fisher 1918, Fisher and Terry 1920). Fisher's work built directly on the extensive observations of Henry Thoreau (1861) (Foster 1999). Both men observed that while pine often comprised the first generation of trees on former agricultural land, it was replaced by shade-tolerant hardwoods and hemlock following logging (e.g., Fisher 1918, 1925, 1928; cf., Spring 1905, McKinnon et al. 1935, Brake and Post 1941, Foster and O'Keefe 2000). The inability of white pine to retain its prominence on most upland sites after disturbance led Fisher and others to question pine's historical role in the landscape, its viability as a timber species, and the ability of foresters to manage it sustainably in the future (Spring 1905, Averill et al. 1923, Gould 1960).

To address these issues Fisher launched a large effort to study the vegetation, dynamics and history of land use and disturbance of the entire Harvard Forest, including the old-growth white pine and hemlock forest in the Pisgah Mountain area of New Hampshire (Fisher 1921; cf., Branch et al. 1930, Cline and Spurr 1942, Foster 1998). Fisher was motivated by his early recognition that information on landscape history and dynamics were critical for interpreting the modern characteristics, management potential and future of any forest (Fisher 1931).

By the early 1920s, Fisher noted that white pine, often in combination with hemlock, appeared resilient to cutting on extremely well-drained sandy sites (Marshall 1927). This observation was of commercial importance because pine was the most valuable timber species in the Northeast and an important part of the rural New England economy at the time (Fisher 1921, Raup and Carlson 1941, Gould 1960, Cronon 1983, Foster and Aber 2004). The observation also generated ecological interest. White pine and hemlock were dominant species of the few remaining old-growth forests in central New England and were interpreted to have been important in the pre-European forest (Nichols 1913, Spurr 1956b, Cline and Spurr 1942, Winer 1955, Whitney 1990, 1993). However, their co-occurrence and persistence remained largely enigmatic (e.g., Fisher and Terry 1920, Merrill and Hawley 1924, Cline and Spurr 1942, Abrams and Orwig 1996). Development of a stronger understanding of the ecology and role of these species on sandy sites therefore offered the promise to resolve these questions and to manage pine and hemlock.

To investigate pine and hemlock co-existence Fisher and his colleagues developed a large and well-coordinated set of field studies on the 61-ha Adams Fay Lot owned by the New England Box Company, a major producer of white pine boxes. The Adams-Fay site, a flat sand plain, was ideally suited for these studies and controlled experiments as the relatively uniform soils supported a fairly homogeneous forest of pine and hemlock. The studies engaged five graduate students, three faculty members, and a six-person woods crew in three related activities. First, the students sampled the entire area intensively and described its history using tree rings and local information. One of these students, Bob Marshall, a subsequent leader of U.S. forestry and founding member of the Wilderness Society (Glover 1986), then investigated the forest's history in detail through an intensive reconstruction of a 0.15-ha plot in the center of the area (Marshall 1927). The historical information formed the basis for an interpretation of hemlock and pine response to logging disturbance and provided the background for a series of experimental harvests (Cline and Davis 1930). The forest harvests were laid out across the area and utilized different intensities and types of logging (e.g., clear cut, shelter-

wood cutting, and selection harvests) and control areas (Lutz and Cline 1947, Raup and Carlson 1941). This coordinated effort explicitly used the historical interpretation of forest dynamics over two centuries to plan, predict and monitor the response of the forest to contemporary silvicultural treatments.

METHODS AND INSIGHTS FROM MARSHALL'S HISTORICAL RECONSTRUCTION. While Marshall's research laid the groundwork for the entire large study, it also provided a basic understanding of the long-term dynamics of the white pine-hemlock forest and the ecological characteristics of hemlock (Marshall 1927, Raup and Carlson 1941). Subsequent researchers adopted the historical approach and methods developed by Fisher and Marshall in a series of well-known studies (cf., Cline and Spurr 1942, Henry and Swan 1974, Oliver and Stephens 1977).

Marshall began by compiling the history of the large forest area using tree rings, historical documents, oral histories and site characteristics, including stumps that he aged and dated. This work documented the dominance of pine and hemlock across the area and provided a general chronology for the logging and regeneration history of the whole forest. It showed that the forest was logged repeatedly, including a series of harvests from 1834 to 1884 (Marshall 1927). In the center of the forest, Marshall then conducted an intensive stand reconstruction in a 80 × 200 foot (0.15-ha) plot to document details of the age structure, compositional history and cutting history based on all living and dead trees. To undertake this work he mapped the topography, living stems, old stumps, and newly cut stumps; cored all live stems > 4 inches (10.2 cm) at stump height (10 inches (25.4 cm) above ground surface); and counted the tree rings on all fresh and decaying stumps. Marshall also aged each log segment in an early effort to reconstruct the height growth of the trees and stand (cf., Stephens 1955, Oliver and Stephens 1977). This reconstruction revealed that the forest largely comprised even-aged cohorts and that both hemlock and pine had persisted through the lengthy history of logging activity (Marshall 1927).

By analyzing the growth rings of pines and especially hemlocks, Marshall developed a detailed understanding of the contrasting regeneration and growth of the two species.

In particular, he documented the remarkable ability of hemlock to persist in shade for more than a century and then grow rapidly when released from suppression, and contrasted this with white pine's pattern of early dominance, moderate shade tolerance and more consistent growth. Based on this understanding of the contrasting autecologies of the two species, Marshall developed a simple model of mixed forest development to explain the maintenance of the two species over time and the age structure and growth patterns that he observed.

"The [early] forest consisted principally of white pine, with considerable hemlock... When one element dropped out either surrounding trees seeded in the spot or advanced growth reproduction replaced the dead tree. But only the most shade-tolerant species could possibly survive...therefore, the understory consisted chiefly of the shade-enduring species, hemlock, which though it grew on the average only about an inch in a century, was nevertheless able to maintain life. It was only when some natural catastrophe made a small opening in the forest that the trees had an opportunity to grow to a large size...Frequently in larger openings the less tolerant white pine would seed in and overtake the slower growing hemlock. Then another period of suppression would ensue." (Marshall 1927, page 9)

Employing this understanding of historical dynamics, Marshall proposed simple silvicultural guidelines for managing these forests for both species. Meanwhile, Fisher, Albert Cline and the other researchers designed the experiments to evaluate the forest response under commercial harvesting conditions (Cline and Davis 1930, Lutz and Cline 1947).

Marshall, Fisher and colleagues collected and archived a detailed series of maps, notes, photographs and data for the entire Adams Fay Lot, including the accurate location of Marshall's intensively studied plot. Large-scale maps for that plot, which depict the location of all of the 19th century and 1924 stumps that he aged, survive along with all of his compositional and age-structure data and plot photographs. These resources allowed us to study the forest, reestablish Marshall's plot, and document the changes since 1924. Eight decades later and following the most intense

natural and human disturbances in the site's history, we used the comparison of historical and modern data to evaluate his conclusions and test his prediction of compositional resilience by this white pine-hemlock forest.

SUBSEQUENT DISTURBANCE HISTORY OF MARSHALL'S STAND. The experimental treatments applied to the larger forest area in 1924–25 included clearcut, group selection (removal of small patches or groups of similar trees), and shelterwood (removal of trees in two or three logging episodes over time) harvests (Fig. 1; cf., Lutz and Cline 1947). Marshall's intensive plot lay in a 2-acre (0.81-ha) area that was harvested by the "group selection" method in which 51 mature trees were removed in small (25–100 m²) even-aged patches. Over the next fourteen years, Harvard Forest researchers inspected, photographed and sampled the harvest and control areas, including Marshall's plot. These data indicate that both hemlock and white pine reproduced, established abundantly and continued to dominate stands across the area. The proportion of the two species and hardwood species varied with the size of individual canopy openings and local edaphic variation, especially soil disturbance generated by the skidding of logs during the harvest and the burning of piles of branches and other slash.

On September 21, 1938, the entire experimental area was severely damaged by the hurricane that swept across New England and blew down approximately 70% of the standing volume of timber on the Harvard Forest (NETSA 1943, Rowlands 1939, Foster and Boose 1992). The Adams Fay Lot was exposed to the full impact of the wind. All of the remaining mature forest on the experimental area was windthrown and most of the trees on Marshall's plot and the other harvested blocks were uprooted, broken, or severely bent. The experiment was terminated and most of the area was logged in a salvage operation that sought to remove merchantable timber and reduce fire hazard. The salvage operation was intensive across this accessible area. The skidding of logs, burning of associated slash, and cutting of many of the remaining live stems added to the hurricane impact to make this the most severe disturbance in the forest's history (cf., Rowlands 1939, Foster et al. 1998). Due to the extent of damage and the young age of the regrowing forest, the area has

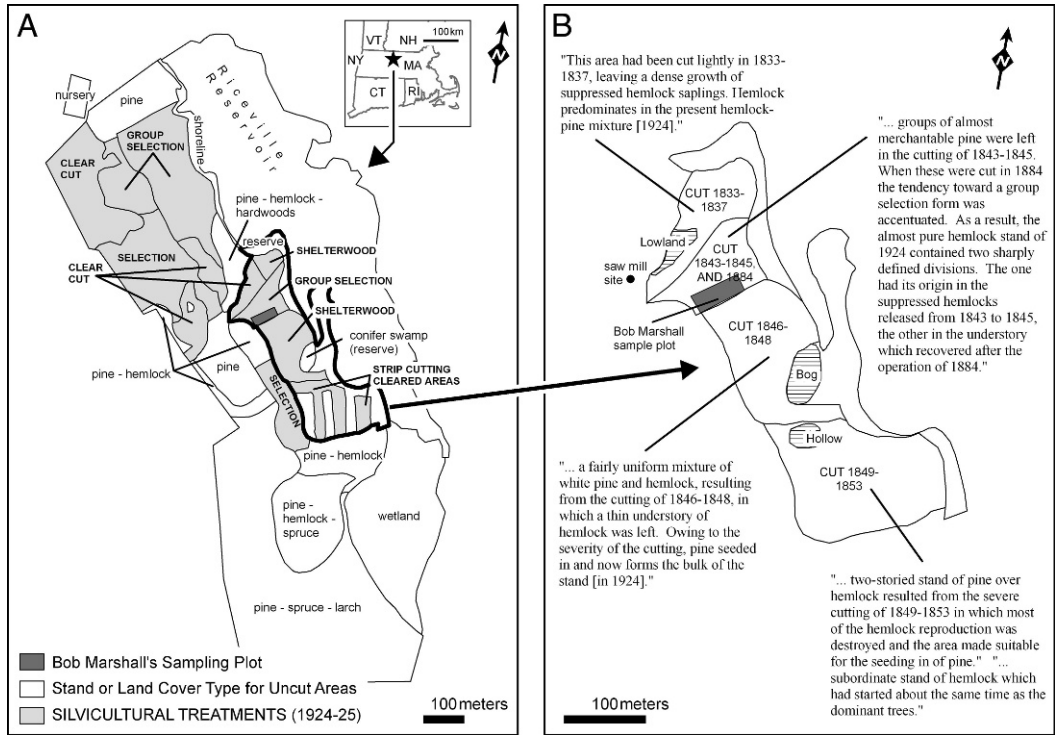


FIG. 1. A. The 61-ha Adams Fay Lot within Harvard Forest and the New England states (inset). B. The treatment areas in the large silvicultural experiment designed on the Adams Fay Lot and the location of the 80×200 foot plot studied intensively by Bob Marshall.

received little attention since the hurricane. A low intensity sample in 1989 of the forests across the area indicated that conifers dominated the composition. In a total of 19 plot-less samples using a $10\times$ prism the average basal area of 191 ft^2 per acre (44 m^2 per ha) was estimated to be approximately 47% hemlock, 30% white pine, and 13% hardwood species (unpublished data, Harvard Forest Archives).

Materials and Methods. **STUDY SITE.** The Adams Fay Lot is a gently undulating 61-ha area of the Harvard Forest Tom Swamp Tract ($42^\circ 30' \text{ N}$, $72^\circ 12' \text{ W}$; Fig. 1) underlain by glaciofluvial deposits (Cline and Davis 1930). The soils are excessively drained Merrimac sandy loams and Merrimac-Hinkley loamy sands. The average elevation is approximately 300 meters above sea level and the aspect is generally easterly towards the adjoining Riceville Reservoir, a narrow water body that lies approximately 10 m below the level of the upland forest (Cline and Davis 1930).

PLOT RELOCATION. Bob Marshall either never permanently marked his 0.15-ha plot or the 1938 hurricane and salvage operations obscured the markers. However, detailed maps of the Adams Fay Lot provide accurate locations, dimensions and compass bearings for the plot, all experimental harvests, and prominent landscape features. In summer 2007, we used these maps to relocate and reestablish Marshall's reconstruction plot and mark it permanently. We divided the plot into 10-foot (0.3 m) grids, mapped all stems, stumps and mounds, constructed a relative elevation map, noted all landscape features and took an extensive series of photographs to parallel and augment the historical pictures. Comparison of these data and observations to those of Marshall and other researchers from the 1920s provided multiple lines of evidence that confirmed the plot placement and allowed the interpretations of long-term changes in the forest.

FOREST INVENTORY AND COMPARISONS. To document the forest composition, compare it

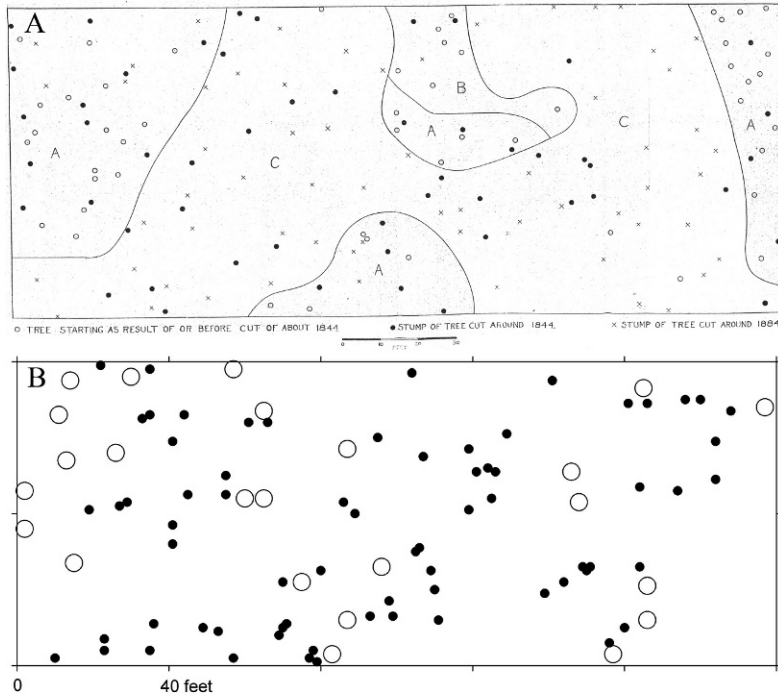


FIG. 2. A. Scanned reproduction of Bob Marshall's original 1924 vellum plot map on which open circles represent stumps of trees cut in the winter of 1924–25, filled circles and Xs represent 19th century stumps. B. Ground surface features in 2007 on which filled circles represent stumps and open circles represent tip-up mounds. The scale is identical on both maps, which utilize Marshall's original English units.

to the historical data and evaluate Marshall's conclusions, we identified and measured all living and dead stems ≥ 2.5 cm DBH for diameter. These data were used to calculate total basal area as well as the basal area, relative basal area, density, and relative density for each species.

STEM MAPPING. In 1924, Bob Marshall described the distribution of mature hemlocks stems in the larger area and his plot as group-like or clumped (cf., Fig. 2A). To document the current stem distribution in the permanent plot the location of all living stems ≥ 2.5 cm DBH were mapped (Fig. 3).

TREE-RING STUDY. To document the current forest age structure, a random subset of 25 live trees ($\sim 1\%$ of total) was cored as close to the base as possible. Annual growth rings were counted under a dissecting microscope to determine the approximate year of recruitment for each stem. One red maple (*Acer rubrum* L.) was excluded from the sample due to heart rot.

Results. **SURFACE FEATURES IN THE BOB MARSHALL PLOT.** Despite precise mapping efforts, it was not possible to match individual stumps directly to those on Marshall's plot map (Fig. 2 B). However, the spatial pattern of adjoining areas of stumps and uproot mounds on the modern map matches well to areas where Marshall mapped the trees cut by group selection and adjoining areas in which trees were retained. The relative elevation in the plot varied by only a few meters and was characterized by a small drainage (< 1 m deep and 2 m wide) oriented northwest-southeast through the plot. This topographic variation also matched Marshall's description.

FOREST COMPOSITION, STRUCTURE, AND AGE. The composition of the forest in 2007 was similar to that in 1924, and to Marshall's prediction, as hemlock and white pine dominated the plot (Table 1). Hemlock had a higher stem density, but white pine had larger average size. Although red maple was the most abundant hardwood species, it comprised less than 4.5 percent of total stems of the current

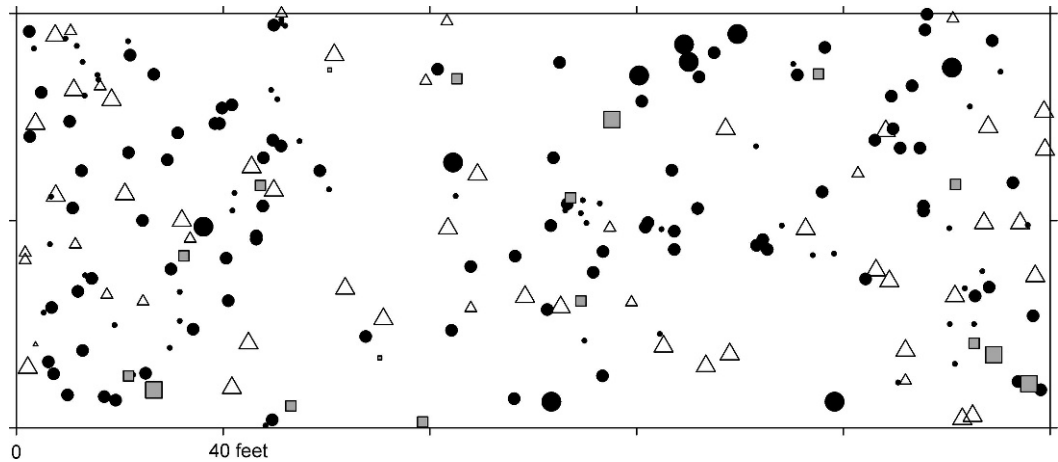


FIG. 3. Marshall's plot in 2007 displaying the spatial distribution of all living and dead tree stems greater than 2.5 cm DBH. Symbols: circles = hemlock; triangles = white pine; and squares = hardwoods. Symbol size corresponds to three size classes: small, 2.5–9.9 cm DBH; medium, 10.0–25.0 cm DBH; large, 25.1–58.8 cm DBH.

forest. In the larger forest area, the distribution of hemlock is clumped, but this is not clearly apparent in the smaller permanent plot (Fig. 3).

Despite the intervening period of intense disturbance, overall composition and plot stand structure in 2007 and 1924 are quite similar (Table 2). The average stem age reported by Marshall was older and the range was much broader: 86 years old and a range of 70–272 years in 1924 compared to 59 years old and a range of 38–84 years in 2007. The 1924 timber cruise of the group selection (1 ha) area including Marshall's plot indicates a greater dominance of white pine in the modern forest: 66% in 2007 versus 14% in 1924 (Tables 2 and 3). Hardwood percentages, which were low in 1924, were even lower in 2007.

Discussion. Across much of the New England landscape, hemlock and white pine display distinctly different patterns of distribution and historical dynamics due, in large

part, to contrasting responses to the history of land-use (Frothingham 1915, Winer 1955, Foster 1988, Barnes et al. 1998). Following regional agricultural abandonment in the late 19th and early 20th century, white pine became abundant across central New England because it dispersed effectively, established widely and grew rapidly on former pastures and fields (Gould 1960). The resulting old-field white pine stands became a prominent part of the regional landscape and a major focus of the regional economy (Fisher 1931, McKinnon et al. 1935). However, pine's intermediate shade tolerance limits its ability to compete with many hardwoods and hemlock in the forest understory. Consequently, when existing pine stands are disturbed the established hardwoods and hemlock have a great advantage over pine, even when a large seed source is available (Fisher and Terry 1920). Over time, logging or windthrow on most moist upland soils gradually lead to the replacement of white pine by more shade-tolerant species

Table 1. Forest composition in the Bob Marshall plot in 2007. The plot is 80 × 200 feet in size (0.15 ha) and values are based on a complete tally of all stems > 2.5 cm DBH.

Species	Live stems	Relative density	Basal area (m ²)	Relative basal area
Hemlock	187	0.67	3.1	0.36
White pine	67	0.24	4.8	0.56
Red maple	12	0.04	0.5	0.06
Red oak	3	0.01	0.1	0.01
Black birch	2	0.01	0.0	0.00
Paper birch	7	0.03	0.1	0.01
Totals	278	1.00	8.8	1.00

Table 2. Structural characteristics of the Bob Marshall Plot in 1924 and 2007. The plot is 80 × 200 feet in size and the values are based on a complete tally of all stems > 2.5 cm DBH.

	1924	2007
Live stems (> 2.5 cm DBH)	270	278
Average diameter	19.1 cm (stump height)	17.3 cm (breast height)
Average age	86 years	59 years
Age range	70–270	38–84

including oak, red maple, black birch (*Betula lenta* L.), beech (*Fagus grandifolia* Ehrh.), and hemlock (Averill et al. 1923, Torrey and Allen 1962, Abrams and Orwig 1996).

In contrast to pine, hemlock is extremely shade tolerant, grows slowly, and has limited dispersal and more restrictive requirements for establishment. These traits give hemlock a relatively slow rate of movement across the landscape and back onto sites where it was historically excluded by deforestation, farming, or fire (Winer 1955, Pacala et al. 1996). Due to its shade tolerance and physiological flexibility, hemlock can establish and persist in the forest understory and then grow relatively rapidly when “released” from shade by disturbance (Merrill and Hawley 1924, Marshall 1927, Winer 1955, Abrams and Orwig 1996). Consequently, in the 20th century white pine was dominant in many young, first-generation forests, whereas sizable hemlock trees were largely restricted to sites that were never cleared for agriculture and were among the least disturbed in the landscape (Spurr 1956a, b, Winer 1955, Foster and Zebryk 1993, Foster et al. 1998, McLachlan et al. 2000). These autecological and historical differences between the species produced striking contrasts in their temporal pattern of abundance through the 20th century. While white pine-dominated forests have declined due to harvesting and disturbances like the 1938 hurricane, hemlock abundance and distribution has increased throughout the region (Foster and Aber 2004).

Fisher and his Harvard Forest colleagues observed that the situation differed on sandy soils where white pine could regenerate successfully and compete with hardwoods and hemlock. Their explanation for this difference was grounded in the greater efficiency of conifers relative to hardwoods to deal with moisture stress on these sites. Marshall’s work on the Adams Fay Lot bolstered this interpretation and his historical research confirmed that both species had coexisted on the site since the 18th century despite a history of logging. Marshall’s intensive stand reconstruction documented the resilience of this white pine-hemlock forest through multiple episodes of disturbance and provided a mechanistic explanation for their unusual coexistence based on their contrasting life histories. White pine was opportunistic, seeding abundantly into new canopy openings, especially large gaps created by harvesting. Once established, pine grew rapidly to form even-aged groups and to become the tallest, dominant trees in the forest. Meanwhile, hemlock established more consistently through time, wherever small openings occurred, and more abundantly in moderate sized openings. While growing more slowly than pine, which rapidly overtopped it, hemlock persisted for decades or even a century or more until increased light from a subsequent disturbance led to an increase in its diameter and height growth. Meanwhile, the hardwood species were less well suited to the dry conditions and less competitive than pine or hemlock. Therefore, although the two conifers

Table 3. Stand composition of the 1924 group selection area and the Bob Marshall sub-plot in that area in 2007.

	1924		2007	
	% Stems	% Conifer basal area	% Stems	% Conifer basal area
Hemlock	70%	86%	67%	34%
White pine	15%	14%	24%	66%
Hardwoods	15%		9%	

displayed distinctly different age structures, growth patterns, and changing abundance, their specific traits enabled them to co-exist and form a resilient forest.

The experiment established on the Adams Fay Lot tested Marshall's interpretation and evaluated the effect of different silvicultural treatments on the relative abundance of the two conifers. While observations in the late 1920s and 1930s supported Marshall's conclusions, the massive impacts of the 1938 hurricane and salvage operations destroyed the experiment. These disturbances also subjected the resilience of the hemlock and pine forest to an extreme test. Although it was no longer possible to make meaningful comparisons across the different treatments and control areas, the comprehensive archive of data and observations enabled evaluation of the long-term dynamics of the larger area and Marshall's plot.

The present study, conducted eight decades after the initial research and nearly 70 years after the hurricane, confirms Marshall's broad conclusions as well as his mechanistic interpretation. Hemlock and white pine continue to dominate the sandy site as predicted. While most overstory trees were killed by the storm and salvage, both species recovered. Scattered understory hemlocks survived the multiple disturbances; in the current stand these individuals display curved stems, broken tops, and other scars produced by direct wind damage or the impacts of falling larger trees. Both species regenerated abundantly after the storm and salvage but the rapidly growing pines outpaced the other species and now surpass all but the very oldest hemlocks in height and diameter. Hemlock dominates the understory and subordinate size classes where it will persist until released, in the pattern documented in detail by Marshall. Meanwhile, the scattered maples, birch, and oaks display three growth forms: multiple-stemmed sprout clumps initiated by wind breakage and salvage logging, curved and broken larger stems that were damaged by the hurricane winds, and falling trees, and single straight stems that presumably established as seedlings after the disturbance. Overall, there is a striking similarity between the forest and Marshall's plot today and their condition in 1924 (Figs. 4 A–C and Fig. 5).

Conclusion. This study, based on revisiting the site, data and interpretations from Bob Marshall's study in the 1920s, confirms the

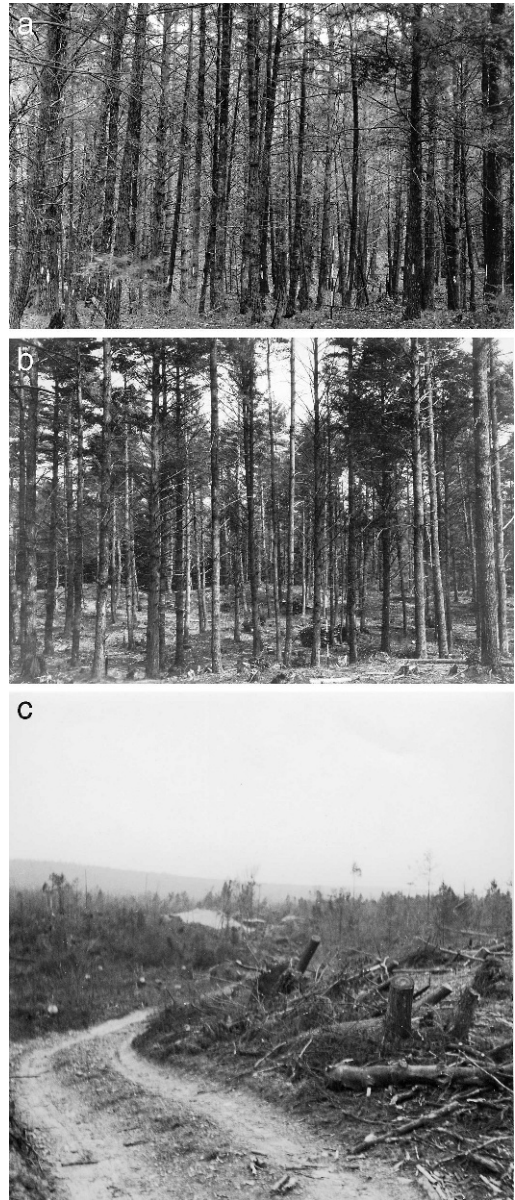


FIG. 4. Historical photographs of the Adams Fay Lot and Bob Marshall's plot. A. The plot in 1924 with trees blazed for harvest and a surveyor's stake is shown for scale. B. Post-harvest forest in 1925 looking across the Marshall plot with the same surveyor's stake for scale. C. Area surrounding the Marshall's plot and looking south in 1940 following the hurricane and salvage operations.

resilience of the white pine-hemlock forest type through multiple episodes of disturbance on excessively drained soils. The work relies on one of the earliest scientific studies of forest reconstruction, a historical approach to eco-



FIG. 5. The Bob Marshall plot in 2007. The dominant trees are hemlock and white pine with scattered red maple, oak, and birch.

logical interpretation that laid the groundwork for subsequent generations of ecologists at the Harvard Forest and beyond (cf., Cline and Spurr 1942, Stephens 1955, Henry and Swan 1974, Oliver and Stephens 1977, Orwig and Abrams 1999). The study also underscores the utility of integrated ecological studies based on historical interpretation, large experiments, long-term measurements, and the permanent archiving of data, photographs, and observations.

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