DO UNHARVESTED ADIRONDACK FORESTS CONTAIN FOREST-INTERIOR PLANTS

A Final Technical Report to the Northern States Research Consortium

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INTRODUCTION

This report describes a research project designed by the Jerry Jenkins and funded by the Northern States Research Consortium under subaward 550-1071980-46886. The field work was done in the fall of 2009, and the analysis and documentation in late 2009 and early 2010. Glenn Motzkin, Stephen Langdon, Michelle Brown and Alan Belford helped with the field work. Glenn Motzkin helped with historical research and interpretation, and Charlie Canham provided edited FIA data and helped with their analysis. Jerry Jenkins supervised the field work, did the data analysis, prepared the graphics, and wrote the report.

ACKNOWLEDGMENTS

We thank the Northern States Research Cooperative for funding, Shingle Shanty Preserve for access to their lands and the use of Steve Langdon, the Adirondack Nature Conservancy for the use of Michelle Brown, Charlie Canham for the use of and help with his Adirondack FIA data, and Jerry Pepper for access to and the benefits of his knowledge of the archives of the Adirondack Museum.

GOALS

The primary goal was to determine whether unharvested Adirondack forests contain plant species which either do not occur or are significantly less abundant in harvested forests. These will be called *forest-interior plants*, indicating that they are species that require, to some as yet unknown extent, continuous-canopy forests and are reduced or eliminated when the canopy is opened or the soils disturbed. The phrase is analogous to the phrase *forest-interior birds*, which is widely used in conservation biology.

A second, more general, goal was to document the structure and the botany of unharvested Adirondack forests. These forests are unique in their extent and relatively little studied. They are an amazing public and scientific resource, and we felt that anything we could contribute to the knowledge and appreciation of them would be time well spent.

IMPORTANCE

The existence of forest-interior plants in the Adirondacks would be of conservation importance. It would:

Demonstrate that the large areas of unharvested forest protected by the New York State Forest Preserve are important reservoirs of plant diversity.

Suggest that unharvested forests elsewhere in the Northeast might be similar reservoirs and thus worth protecting.

Suggest that forest managers and holders of forest conservation easements might be able to increase plant biodiversity by creating ecological reserves or managing forest for late-successional structure.

Conversely, finding that forest-interior plants do not exist would also be important. It would:

Focus attention on other components of biodiversity and on other reasons for protecting unharvested forests.

Suggest that the highest diversity Adirondack forests may be found on lands that are not currently protected.

Suggest that future research will be needed to find and protect these forests.

CURRENT KNOWLEDGE

Adirondack forests have received significant historical, ecological, and silvicultural study. They have, however, received much less botanical study. The historical studies are few and scattered. The largest bodies of recent work are studies by the author and his colleagues in the Champlain Hills, and by Mike Kudish in the northern Adirondacks and High Peaks*. Little of the botanical work has examined the large tracts of unharvested forests in the Central Adirondacks which are the focus of this study.

* See Jenkins (2004-2007), Kudish (1992) and the references in Kudish. Also McGee et al. (1999) for a structural study of forests similar to the ones we worked in and McGee and Kimmerer (2002) for bryophytes in old growth..

The literature on forest-interior plants, Adirondack or otherwise, is sparse and to some extent confused. I have examined it elsewhere*, and won't repeat the analysis here. Suffice to stay that while there are numerous studies of the effects of harvesting on plant diversity, few have had adequate historical or taxonomic resolution, fewer have focused on the behavior of individual species, and none have had the benefit of the large areas of unharvested forest that we have in the Adirondacks.

* Jenkins (2007, 2008)

Thus, at the time we commenced this project, our knowledge of the flora of Adirondack old-growth forests was limited, and our ability to compare the floras of old-growth and harvested forests almost nonexistent.

DEFINITIONS

For the purposes of this study a *forest-interior plant* is a vascular plant or bryophyte that

a is widely distributed in Adirondack forests,

b is more common in forests than in other communities, and

c is significantly more important in unharvested forests than in ones that have been repeatedly harvested.

These conditions are fairly restrictive. Conditions *a* and *b* define what we mean by a forest plant. *A* says that we are only interested in plants that are regular members of the forest community and thus contribute to overall forest diversity. Extremely rare species are excluded, both because it is impossible to get enough data about them to measure their distribution and because they contribute very little to overall diversity. *B* says we are only interested in true forest species, and not species from, say, wetlands or open summits that occasionally occur in forest interiors.

Condition *c* defines what we mean by an *interior* species: not any plant that grows under forest canopies, but rather one whose abundance is greatest in the stands with the least human disturbance.

Note that none of the conditions say that forest-interior species must always grow under canopy. Small gaps are common in all forests, and observation suggests that almost all forest plants, even the most shade-tolerant, do well in them.

METHODS

The overall plan was to sample vascular plants and bryophytes in study areas with three different histories: *early acquisition* forests that have been in the New York State Forest Preserve since before 1900; *later acquisition* forests that were added to the Forest Preserve after 1900, and *commercial forests* that have been harvested repeatedly in the 20th century.

The logic of the sampling was that, as first worked out by Barbara McMartin*, the date at which New York State acquired a property is a good predictor of how much harvesting the property has had. In this study we call the amount of harvesting the *condition* of the property.

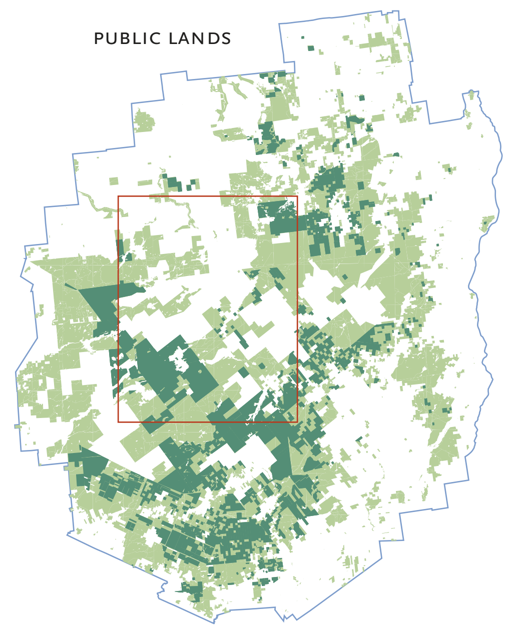
*McMartin (1994).

The correlation between acquisition data and condition works because early Adirondack forests were difficult to access. The central Adirondacks, where we worked, had no railroads until 1892 and almost no logging railroads until 1900. Hence almost all 19th-century logging was river-based and took only large softwoods, particularly pine and spruce. Logging for pulp and hardwoods, both of which were more intense and less selective, didn't begin until the late 1890s and didn't become truly intense until the early 1900s. Logging with tractors and trucks, which reached many areas where there were no railroads, didn't begin until the 1920s.

As a result, the central Adirondacks are a mosaic of three different forest histories. The dark green areas in the map, the early acquisitions, either have never been logged or were logged selectively for large-diameter softwoods before 1900. They are now protected by Article 14 of the state constitution, which says that the timber on Forest Preserve lands may not be sold, removed, or destroyed, and so have not be logged since acquisition*. They should thus, as Barbara McMartin conjectured, contain large areas of old-growth hardwoods. One of our goals was to test this conjecture.

The lighter green areas are 20th century acquisitions that may or may not have been logged before they were acquired and have not been logged since acquisition. Their acquisition date is a rough predictor of their history–any land acquired after 1940 has almost certainly had at least one episode of heavy logging–but only a rough predictor. We call them, generically, lands with *no recent harvesting.* To get a more accurate sense of how much they were cut prior to acquisition we have consulted historical maps and documents, and relied heavily on the archives of the Adirondack Museum.

Finally, the white areas are private lands. All but very small parts of these have been cut at least once. The first cuts of the most accessible lands occurred early in the 1800s; those of the least accessible may have occurred as late as the 1930s. Only small areas remained uncut by the 1950s. We call these lands, again generically, *harvested lands.*



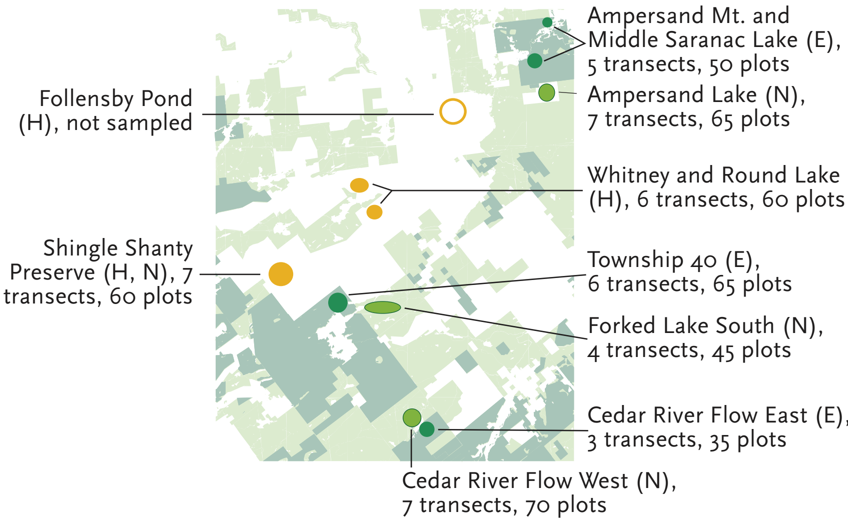
Map adapted from Jenkins (2004). The red rectangle is our study area, shown in the map on p. 6.

Study Areas We selected study areas that were at similar elevations and reasonably near one another, had large (1,000 ha or greater) continuous tracts of hardwood forest, and had good access and well documented histories. Because we wanted to focus on the effects of harvesting, we avoided areas where there had been large blowdowns or fires. And because we wanted to study the plants inside the forests that follow harvesting rather than those in harvested openings, we avoided sites that had been harvested within the last 15 years.

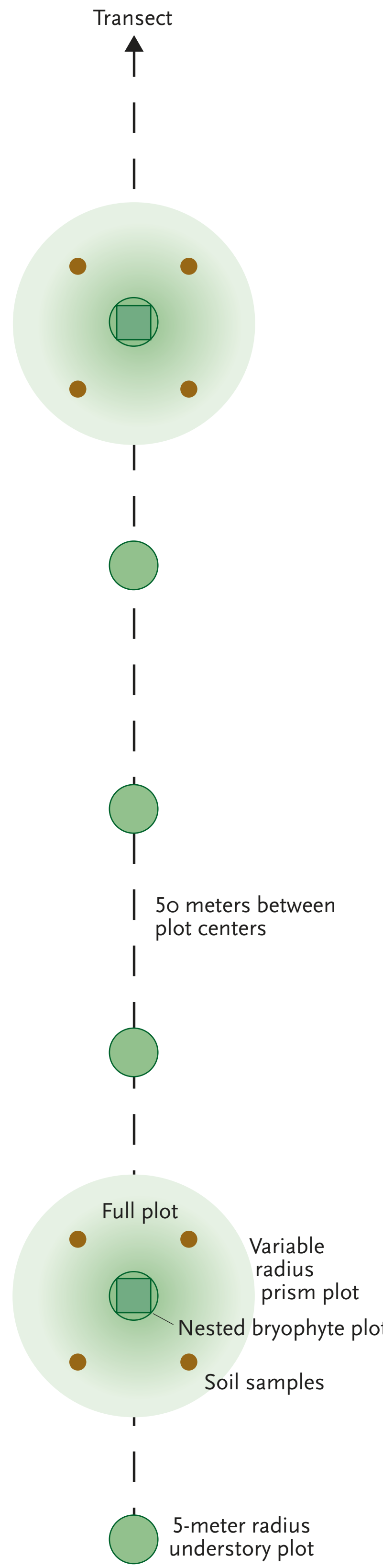
Our goal was to sample 9 forests, 3 early-acquisition (E), 3 with no recent harvesting (N), and 3 that had been harvested within the last 30 years (H). We lost access to one of the harvested sites because of potential conflicts with leaseholders during hunting season and were not able to replace it. As a result our coverage is uneven. We have 2 sites and 120 plots on harvested lands, 3 sites with 150 plots on no-recent-harvest lands, and 3 sites with 180 plots on early-acquisition lands. We regret not having the third harvested site, but since our goal was to find out what

* Some parts of the Forest Preserve were logged, in defiance of the constitution, following the 1950 blowdown (Jenkins, 1996). We did not work in any of these areas.

STUDY AREAS



SAMPLING DESIGN



was on the unharvested lands rather than what was not on the harvested ones, it probably is not too important.

Sampling The sampling design is shown to the right. At each site we laid out a series of transects in upland hardwood forests, with 5 to 15 plots spaced at 50-meter intervals along the transect. Plots were restricted to mesic soils in areas with at least 30% wood cover, and had to be at least 10 meters from the edge of a road, large gap, or wetland.

After some initial experimenting, we developed a pattern in which the first plot and every fifth plot after that was a full plot, and the remaining plots were understory plots.

At the full plots we took a pooled soil sample, listed all the trees accepted by a factor-5 English prism, measured the diameters of these trees with calipers, listed all the shrubs and herbs in a 5-meter radius (1/127 hectare) circular plot, and took data on bryophyte substrates and cover as described below.

At the understory plots we listed vascular plants and determined the total basal area with a prism, but did not take soil samples, measure individual trees, or take bryophyte data.

At all plots we recorded slope, aspect, GIS coordinates, canopy and subcanopy cover and composition, and notable features of substrate and vegetation.

Vascular Plant Data In each 5-meter understory plot we identified all the herbs and shrubs, and recorded their abundance using a 4-part scale:

1 Rare in the plot, only a few individuals present.

2 Commoner, but only a few 10s of individuals or less than 1 sq.m cover.

3 Throughout the plot, or with a square meter or more of cover.

4 With significant coverage, several square meters or more, in all parts of the plot.

Most vascular plants were identified to species. This was possible because the species pool of upland forests is small, with under 100 species. Almost all of these, including all the grasses and most of the sedges, can be identified vegetatively. The major exceptions were:

Stemless white and blue violets, lumped as *Viola sp.*

Carex novae-angliae and one or more of its rare relatives, lumped as *C. novae-angliae.*

Carex brunnescens, C. convoluta, and *C. appalachica,* lumped as *C. brunnescens.*

Carex seedlings, recorded as *Carex sp.*

Pyrola elliptica and *P. chlorantha,* lumped as *Pyrola sp.*

Bryophytes Bryophytes are hard to see and harder to identify in the field. Most can be determined to genus with a lens, but many need be collected and examined under the microscope to determine the species. Because of this, thorough bryophyte surveys are quite slow–even a highly skilled worker might require several hours to do a relatively small plot where the bryophyte cover was high.

We did not have the time to do this in our survey, and so decided to test a reconnaissance technique, admittedly crude, to see if it produced useful information. The protocol went like this. At every fifth plot a 7.1 × 7.1 meter square (1/200 ha) was inscribed in the 5-meter radius circle. The area of each rock, log, tree base, and stump within the square was estimated by approximating the dimensions to the nearest 0.1 meter, and the bryophyte cover estimated using 5 cover classes: 0%, 25%, 50%, 75%, and 100%*. All dominant bryophytes (ones covering 0.01 sq.m or more) were identified to genus or, for the most conspicuous species, to species.

* On tree bases and stumps only the lowest 20 centimeters was considered.

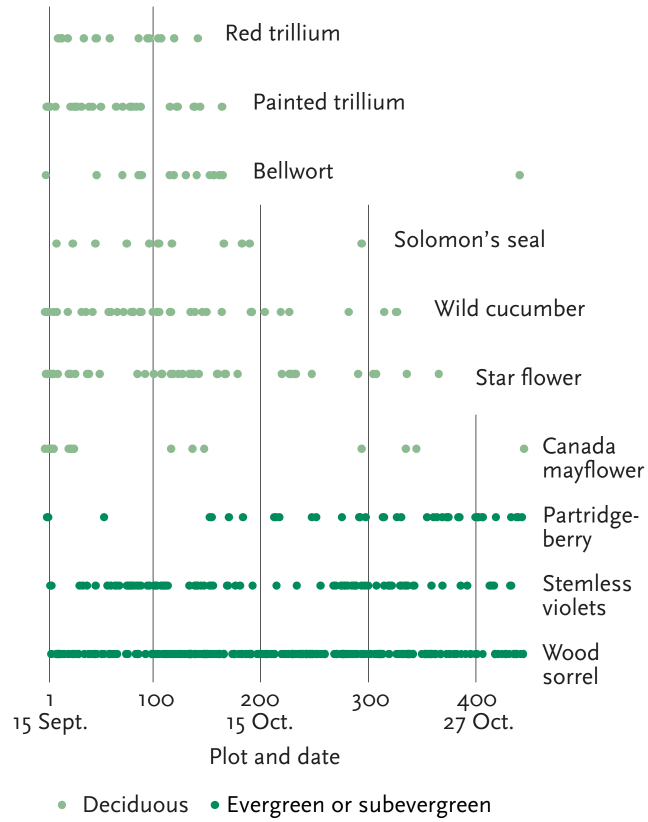
We need to stress that, even with these simplifications, the moss data are somewhere between approximate and sloppy. Rocks, logs, and the bottoms of trees are complex three-dimensional shapes; projecting them onto to a plane and approximating the dimensions introduces serious inaccuracies. Many of the commonest species of mosses can't be identified in the field: thus we had to lump most species of *Dicranum, Brachythecium, Plagiothecium, Mnium sensu latu,* and *Polytrichum*, five genera which can make up over half the bryodiversity of ordinary woodlands.

A further problem, even more basic, is that on dark wet days, which we had many of, it is very dark on the forest floor and it can be surprisingly hard to recognize even the common species, let alone estimate their cover. It may be possible to overcome this by using a strong headlamp. We didn't recognize the problem until it was upon us, and by then it was too late.

Field Work Our field crew was normally three people. One, usually Jenkins, was responsible for the site descriptions, GIS coordinates, and the bryophyte surveys. The other two measured the trees, took the soil samples, and recorded the understory vascular plants. Depending on weather and terrain we did one or two transects and anywhere from 10 to 25 plots a day.

Our first plot was done on September 14, 2009, and our last one, number 450, on November 30, 2009. We had planned to work earlier in the season–July, August, and September are ideal for Adirondack sampling–but Jenkins wore out a knee in the fall of 2008, and had it replaced in June, 2009. (For the record, the new knee worked very well. My first full day of fieldwork was the 87th day after surgery, and my first day on this project the 97th day.)

LOSS OF DELICATE HERBS DURING OCTOBER, 2009



Accuracy of Plant Identifications All botanical field work is inherently imprecise. There are two sorts of problems–the species that you see and the ones you don't.

The ones you see are usually the smaller problem; every flora contains sterile species, but with practice most of these can be identified, and the remainder accommodated, as we did here with some sedges and violets, in enlarged categories. Jenkins and Motzkin have over 70 years of field work between them, and feel reasonably sure that, in the relatively simple flora we were dealing with here, we were identifying 99% or more of the species we saw correctly.

The larger problem is the species that aren't there, either because they are gone or haven't appeared yet. In our there are two problematic groups: the spring ephemerals, and the delicate herbs that senesce after the first frosts.

Only two spring ephemerals, trout lily and spring beauty, are common in the sort of woods that we were studying; others like squirrel corn and toothwort occur rarely. All are gone by the second week in June and will be missed by any survey that is late enough to pick up the major summer species. We have not seen any data at all on their abundance in the central Adirondacks, and hope to do a preliminary survey of them next spring.

At least seven common woodland herbs, shown in light green in the graph above, disappear almost completely a week or two after frost. We had frost (and snow) in early October this year, and lost most of these herbs by October 15. The graph shows that all were reasonably abundant in September and scarce or absent by late October.

None of these herbs are exceptionally common, and we will argue on p. 30 that they don't have much statistical affect on overall herb diversity, and that none are likely to be forest-interior species. But still their loss represents a gap in our data, and one we would like to remedy in further studies.

Excepting the spring ephemerals and delicate herbs, most of the woodland herbs persist into mid-fall. They become shriveled and harder to see, but they are still there, and, as our data on species like wood sorrel and violets show, can be found if you search carefully.

Soil Analysis Soils were gathered from every fifth plot with a 30 cm tube sampler. The O layer was discarded and samples from the different quadrats of the plot pooled to give a total sample of 100 g or more. The samples were stored in plastic bags, air dried and sieved, and sent to Brookside Laboratories in Ohio for analysis for major elements, pH, organic matter, and base saturation.

Data Analysis Data from the 450 plots were entered into Splus datafiles and then averages and standard errors calculated by transect, site and forest condition. Graphs were prepared in Splus; final graphs and the other illustrations in this report were prepared in Adobe Illustrator. The differential distributions of species were examined graphically; the relations between variables were examined with linear regressions and the significance of differences by plotting standard errors..

Data Density and Scale of Analysis Our total data sets consists of:

450 plots with data on slope, aspect, vascular plants, and total basal area,

385 plots with a data on canopy and subcanopy cover,

100 plots with data on bryophyte substrates and cover,

94 plots with measurements of individual trees, and

92 plots with soil analyses.

These plots are grouped into 45 transects at 8 sites, representing 3 different forest conditions (map, p. 6).

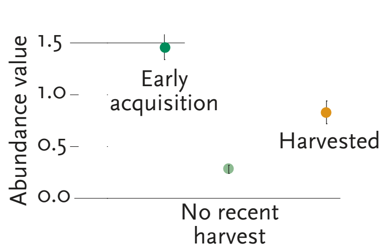
The scale of our analysis–by transect, site, or condition–was determined by the number of plots available. Although our general interest was in the large-scale differences between the three forest conditions, to interpret this we needed to account for the finer-scale variation. Thus we analyzed the data at the finest scale that had reasonable statistical power. For vascular plants, canopy cover, and basal area, this was the transect scale. For bryophytes, soils, and forest composition, it was the site scale.

The importance of fine-scale analysis is illustrated by the graphs at the top of page 10, showing the importance of hobblebush at two different scales. At our largest scale, comparing the three forest conditions, (left graph) there seems to be a clear effect of forest history. Hobblebush is most abundant in early-acquisition forests, less abundant in harvested ones, and least abundant in ones without recent harvests.

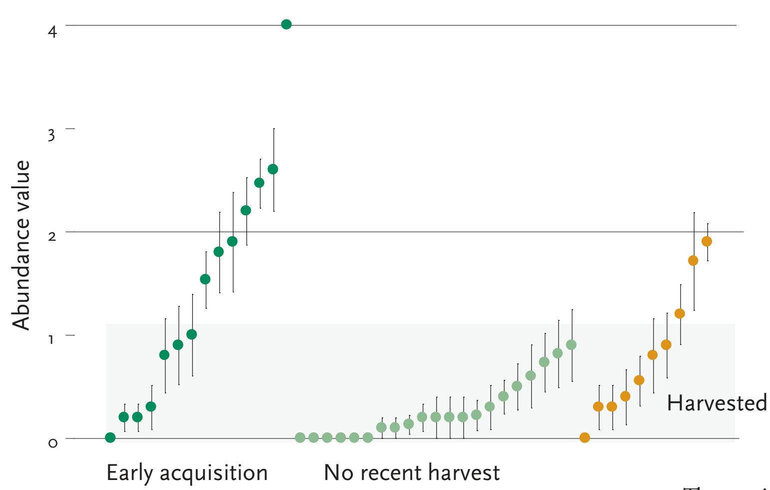
At a smaller scale, shown in the comparison of transects in the right graph, the situation is much less clear. Transects in early-acquisition forests differ much more among themselves than the means for the three conditions. Some have no hobblebush, some have little else. Furthermore, 35 of the 45 transects lie in the shaded area where all three conditions overlap. Had we confined ourself to these 35 transects, which surely would have been a reasonable sample, we would have seen little difference between the means for the three conditions.

Two conclusions follow from this. Both are important. First, there is a lot of this sort of fine-scale variation in abundance, and we have no idea what controls any of it. And second, given that the differences between the much transects are greater

HOBBLEBUSH BY CONDITION



HOBBLEBUSH BY TRANSECT



The vertical lines through the data points, here and elsewhere, are plus and minus 1 standard error.

than the differences between the conditions, our conclusions about the conditions will depend on which transects are included in the sample.

The second conclusion says that when inter-transect variation is high, we need to be very cautious about how we interpret the differences between sites and conditions. This is worth stressing: *In a study like this, with much variance between transects and much overlap between conditions, the mean differences between conditions are very sensitive to selection effects–that is to where we happened to sample. The significance of apparent differences between the three conditions must always be judged in relation finer-scale variance between sites and transects.*

It would be easy to quantify this by bootstrapping the transect and site means. Had we found a group of plausible candidates for forest-interior species we would have done this. We didn't, and so we didn't.

Modeling Study Our original plan, contingent on detecting forest-interior species and getting FIA phase-3 inventory data, was to do two modeling studies, one trying to account for differences in the abundance of forest-interior species and the other comparing Adirondack understories to those elsewhere in the Northeast. Neither was possible. We found no clear forest-interior species in the forest we studied. And while the Forest Service has been gathering phase-3 data for several years, little of this data has been edited or distributed. As of December, 2009, the FIA web site listed only 20 phase-3 plots in the whole Northeast.

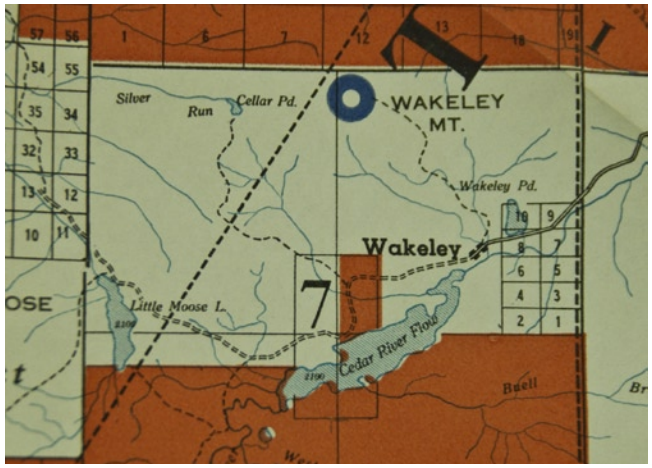
RESULTS: SITE HISTORIES

Because the relation between acquisition date and logging history is only approximate, we researched and attempted to reconstruct site histories from historical maps and documents and interviews with owners and foresters. This is an on-going project. Here is what we have learned so far*.

*Sources for this section are McMartin (1994, 2004); Gove (2006); Graves (1899); Hosmer and Bruce (1901); Meigs (n.d.); Ricknagel (19xx); Kim Elliman and Steve Langdon, personal communications; and maps in the archives of the adirondack Museum.

Cedar River Flow East Early acquisition. Purchased by NYS sometime between 1891 and 1893. Prior logging history not known. Wakely Dam, which created the Cedar

Flow, was in existence by 1890, and used to supply water for drives on the Hudson River. It is likely that the Cedar River was driven as well.

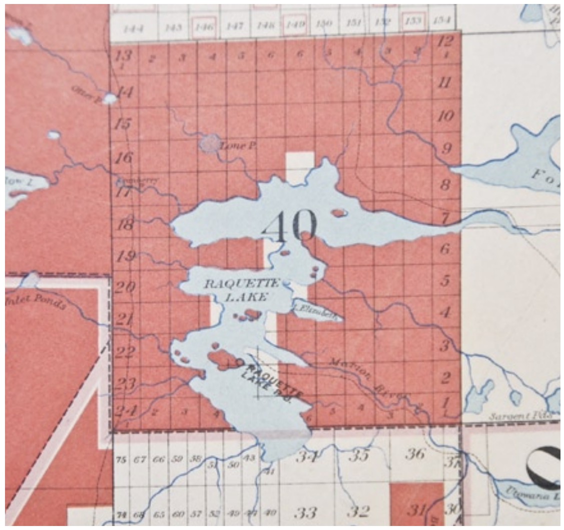


Section of the 1953 Forest Preserve Map, from the collection of the Adirondack Museum.

Cedar River Flow West No recent harvest. The lands in the white square labeled Wakely Mt. (northeast corner of Totten and Crossfield Township 7, were owned by Finch Pruyn. In 1931 they contained virgin hardwoods and second-growth softwoods. They were acquired by New York State after 1983.

Section of the 1916 Fire Protection Map, from the collection of the Adirondack Museum. The slighter darker colors are areas that were cut before 1916; the cabin symbols are lumber camps, with the number of men indicated below them.

Shingly Shanty Preserve Harvested. The Shingle Shanty Preserve is part of Totten and Crossfield Township 39. There are no drivable streams, and all timber from the property is shipped overland. It was acquired by Benjamin Brandreth in 1851; first logged heavily, by railroad, between 1912 and 1920; logged again to supply a sawmill at Brandreth Station between 1925 and 1931; cut for pulp in 1942; cut for hardwoods, perhaps for the first time, in 1943; sold to International paper in 1976, logged by them until 1997, sold to the Adirondack Nature Conservancy in 2000, and bought by the Friends of Thayer Lake, who lease it to the Shingle Shanty Preserve and Research Station, in 2008.



Section of the 1893 Forest Preserve Map, from the collection of the Adirondack Museum.

Township 40 Early acquisition. This is the township south of Shingle Shanty and Brandreth. It was purchased by NYS between 1891 and 1893, and is described as densely stocked, virgin forest in a report by Hosmer and Bruce in 1901. Except for some of the developed shores, there are no records of any historical logging at all.

Section of the 1916 Fire Protection Map, from the collection of the Adirondack Museum.

Forked Lake South No recent harvests. Acquired by NYS around 1900. Logged for softwoods prior to acquisition, and the logs driven down the Raquette River. Probably no hardwood harvests at all. Its history is thus more comparable to the early-acquisition lands than to the other no-recent-harvest lands, and may be analyzed with other early-acquisition lands in future work.

Round Lake and Whitney Harvested. Part of a 68,000-acre tract acquired by William Whitney and Patrick Moynehan in the late 1890s. The tract was logged for spruce between 1898 and 1907 and the logs driven by the Bog River to Tupper Lake.

Map of a portion of Whitney Park, from Graves (1988). The darker, hatched areas have been cuit for softwoods. No hardwood logging had taken place.

The northern parts, where our transects were, may first have been heavily cut for hardwoods between 1936 and 1939, when Whitney Industries built a logging railroad on the grade of the old Mic-a-Mac Railroad through Brandreth Park and into Whitney Park. The lands have been cut several times since; Jenkins examined them in 1988 and 1989 and found very little merchantable timber of any kind. The portion of the land north of the Sabattis Road, including Round Lake was sold to International Paper (date not known) and then to the Adirondack Nature Conservancy and NYS. The lands around Little Tupper Lake and Rock Pond were sold to NYS in 1998.

Section of the 1893 Forest Preserve Map, from the collection of the Adirondack Museum.

Ampersand Mountain and Lower Saranac Lake Area Early acquisition. Early logging history unknown, but the Saranac River was used for log drives by the 1840s, and it is likely that spruce was cut near the lakes. The area around Ampersand Mountain was purchased by William Stillman for a private club in 1858, then repossessed by the town for unpaid taxes, and then part of a large tract in Township 24, that was acquired by NYS in a tax sale in 1877, and has not been logged since.

Section of the 1953 Forest Preserve Map, from the collection of the Adirondack Museum.

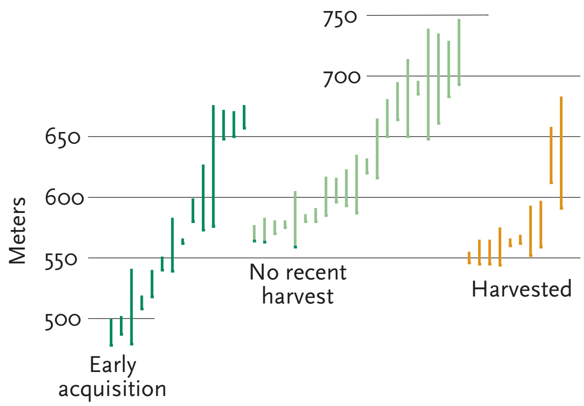
Ampersand Park. No recent harvesting. Ampersand Park, the 3,800-acre tract shown in white above, is privately owned but has not been harvested for 70 years. The land was acquired by the Santa Clara Lumber Company, a large company that was active in the Adirondacks from 1888 to 1941, in the early 1890s. They built a logging camp on the west shore of the lake in 1897, and drove spruce down Ampersand Brook to the Raquette River and their mill in Tupper Lake till 1936. This may have been the last sawlog drive in the Adirondacks. The property was bought by Avery Rockefeller in 1938 and is owned by his descendents today. It has not been logged since it was acquired in 1938. The Santa Clara Company likely cut hardwoods here as well–they had hardwood mills, and Rockefeller family tradition says they took sugar maple but not yellow birch–but we have no clear record of this.

Summarizing, the histories of our 8 study sites, as best we have been able to determine, look like this:

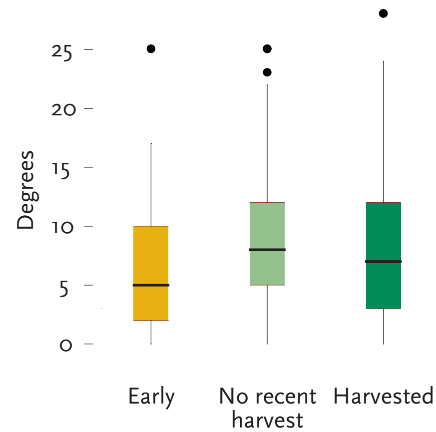
	Cut for softwoods	Cut for hardwoods	Last cut
Early acquisition			
Cedar River East	?	no	1890
Township 40	no	no	
Ampersand Mountain	probably	no	1877
No recent harvest			
Cedar River West	yes	yes	?<1990
Forked Lake South	yes	no	<1900
Ampersand Lake	yes	yes	1936
Recent harvests			
Shingle Shanty	yes	yes	1990s
Round Lake and Whitney	yes	yes	1980-2000

All of these lands thus fit Barbara McMartin's paradigm: the early acquisition lands have early softwood cuts or none, the later acquisition ones several cuts for hardwoods and softwoods, the commercial timberlands many cuts.

ELEVATION RANGES OF TRANSECTS



DISTRIBUTION OF SLOPES



In this and other box plots, the black line is the median, 50% of the data points lie within the colored box, and 99% within the range spanned by the line.

RESULTS: PHYSICAL FEATURES OF PLOTS

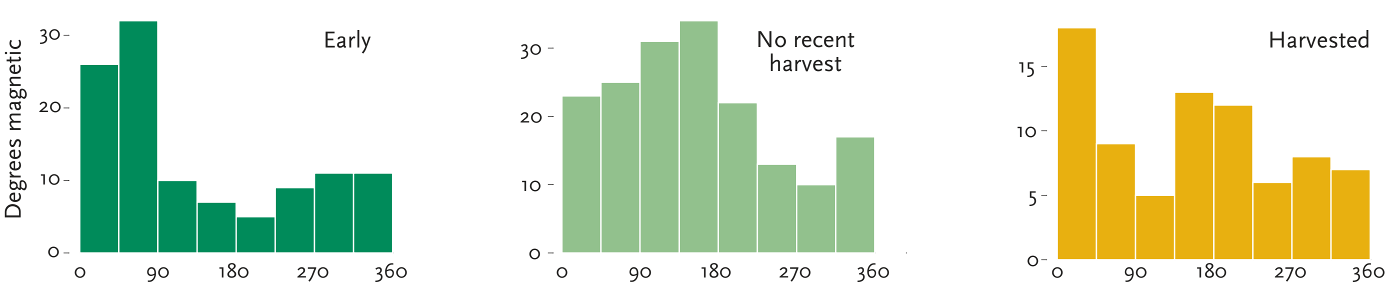
The physical features at our study sites were broadly typical of central Adirondack forests. I show them here mostly to demonstrate that they differed little between the three forest conditions.

Elevations ranged from about 500 to 750 meters. The lower limits was set by the drainage network, with the early acquisition sites at Ampersand Mountain in the Saranac basin lower than the other sites in the Raquette and Hudson basins. The upper limits were set by the ridgetops or, on large hills, by the elevation at which conifers started to dominate.

The slopes at all sites were strongly concentrated in the 3 degree to 10 degree range. Steep slopes are rare, and often have ledges and conifers. Flatter slopes are more common, but tend to be wetter (and thus outside the boundaries of this study) and usually conifer-dominated as well.

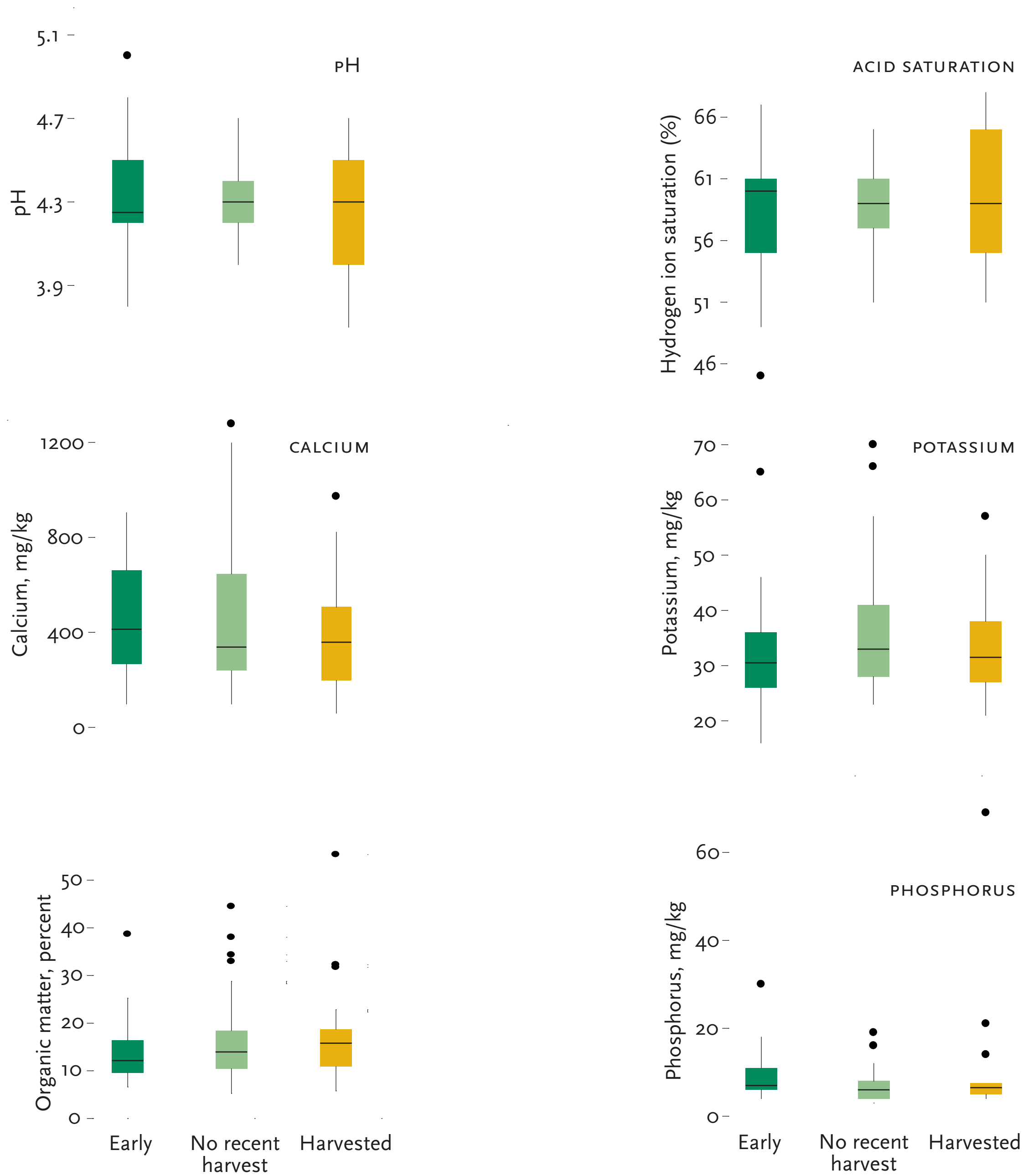
Plot orientations are broadly distributed, except in the early acquisition plots where a number of our transects tended to face northeast. We were unable to detect any effect of this, either in the field or in the data.

DISTRIBUTION OF ASPECT (ORIENTATION)



Soil Structure and Chemistry Structurally the soils were quite similar. Most were sandy loams with a shallow (1-3 cm) organic layer, a thin (3-4 cm) A-horizon, an

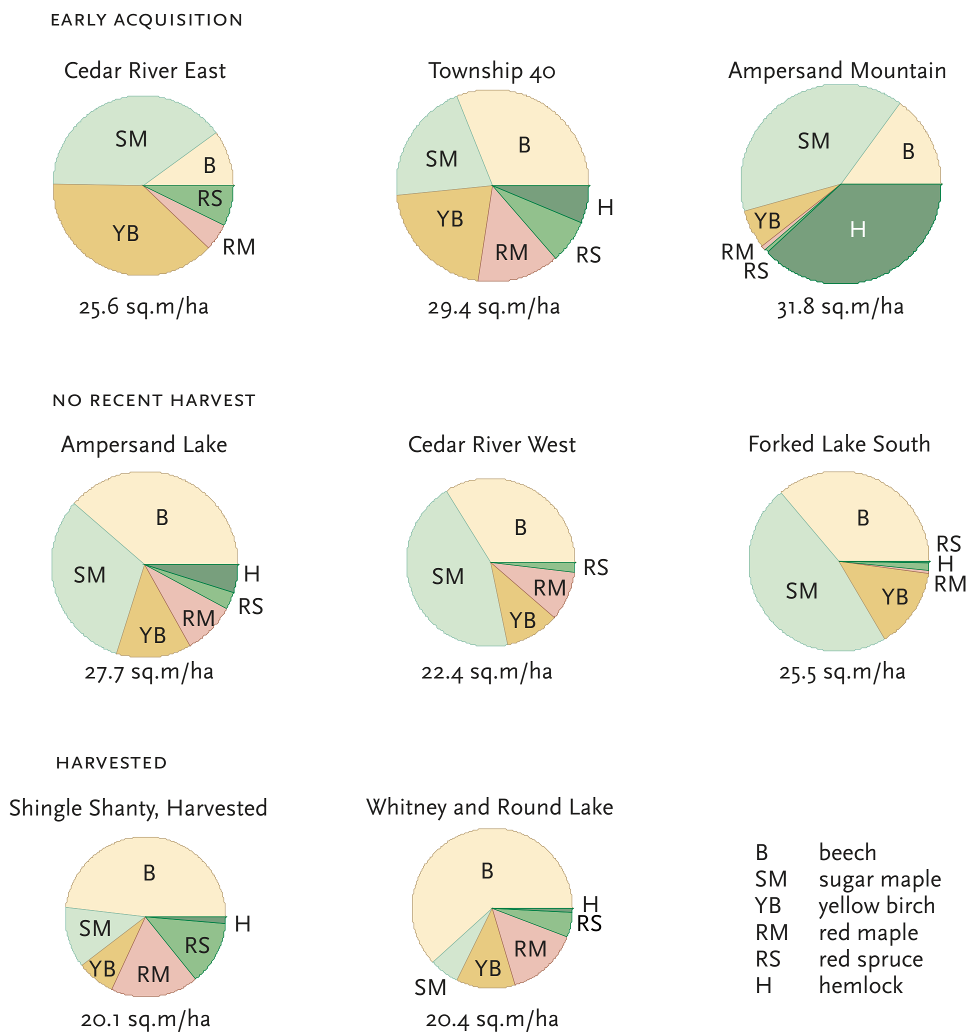
SOIL CHEMISTRY BY FOREST HISTORY



E-horizon of variable thickness showing weak to moderate leaching, and, when our samples reached deep enough, a brighter, brown-red B- or BHs-horizon. We observed variation between plots, but no consistent variation between sites or forest conditions.

The chemistry was similarly uniform. Most were acid woodland soils with pHs under 4.5 and correspondingly low amounts of calcium and potassium and a correspondingly high percentage of the exchange sites carrying hydrogen ions. They had moderate amounts of organic matter but much less than would be encountered in conifer-dominated lowland sites. They showed physical evidence of leaching and chemical evidence of base-cation depletion, but they were not nearly as acidified as some western Adirondack soils where the base saturation may be under 20%.

BASAL AREA BY SPECIES AND SITE



RESULTS: FOREST STRUCTURE AND COMPOSITION

The forests we examined had both strong similarities and strong differences.

We start with the similarities. The majority of the 385 stands for which we have detailed descriptions had four features in common:

They were dominated by just six species, four hardwoods and two softwoods.

Their canopies were discontinuous and their overall canopy cover was less than 50%.

Their subcanopies and understories were usually dense and almost always dominated by young beech.

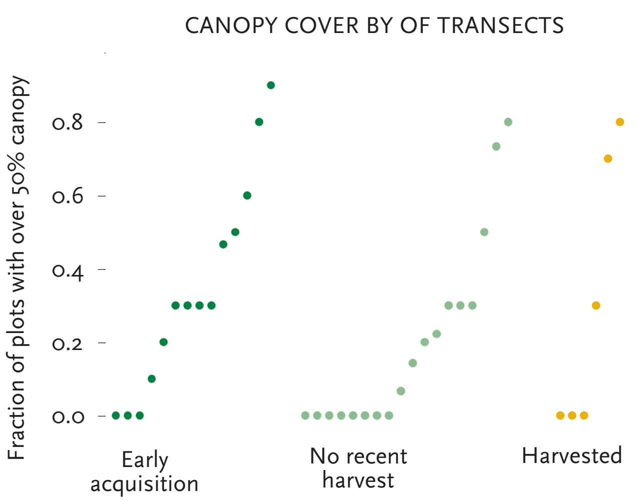
With the exception of red spruce, young trees of other species were uncommon and scattered, though occasional plentiful in small areas.

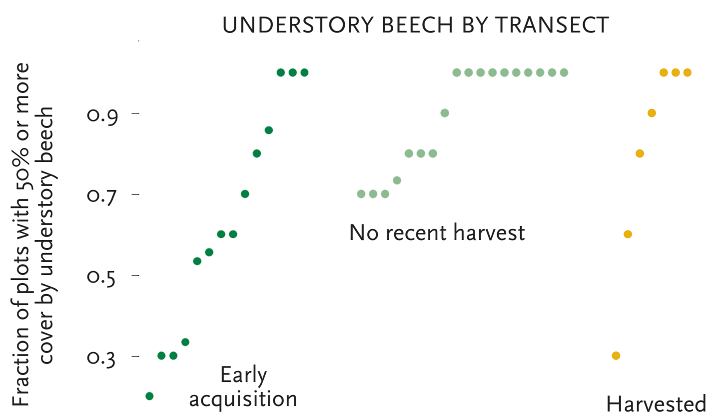
The graphs above and on p. 18 illustrate these features.

Composition and Cover The dominant canopy species were always some mixture of beech, sugar maple, red maple, yellow birch, red spruce and hemlock. Scattered white ash, white birch, and black cherry occurred, but were never more than a few percent of the overall basal area. White pines and quaking aspens, locally common elsewhere in the Adirondacks, were rare here and almost never turned up in our plots.

The pie graphs on p. 17, which are scaled by basal area, show the average forest composition at the different study sites. There are some interesting differences. Beech is common at all sites, but most so at the harvested sites and least so at the early acquisition sites. Sugar maple and yellow birch reverse the pattern, and are commonest at the early acquisition and no-recent-harvest sites.

With other species the pattern is less clear. Red spruce and red maple are variable but do not consistently favor one type of site or another. Hemlock is extremely variable. Our study, which was focused on hardwoods, says little about its distribution.





We did not make canopy cover estimates at Shingle Shanty, and so there are only 7 transects from harvested sites.

The left-hand graph above shows the percentage of plots in which the canopy, defined as the layer containing the tallest trees, is over 50% complete. Continuous canopies, with the tallest trees touching one another, are uncommon. Most of the stands we sampled, irrespective of forest history, had two stories. The upper stories had lost trees to disease or harvesting and were either patchy or contained only scattered trees. The lower stories contained younger trees that were released by the loss of canopy trees.

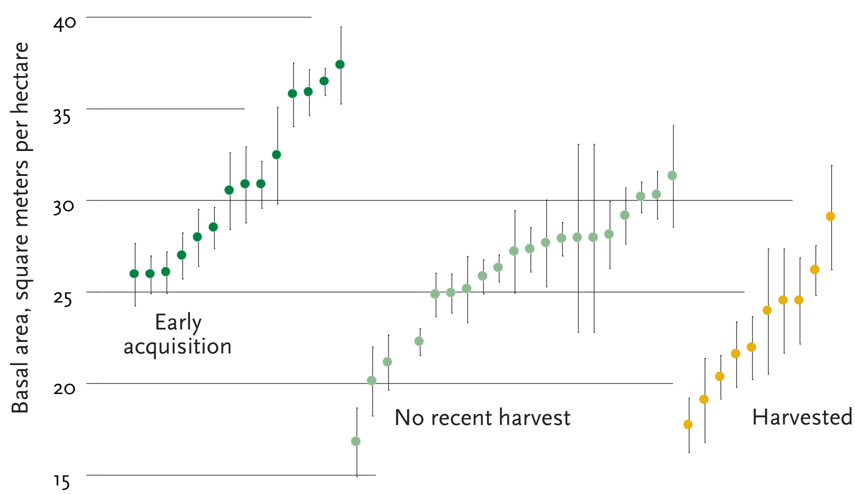
What the high canopies lacked the understories made up for. Most of our sample plots, again irrespective of their history, had dense understories of young beech (right-hand graph, above). Ninety percent of the stands had dense layer of understory beech with a cover of 50% or more. The only exceptions were a few early-acquisition stands where, for some reason, there had been few large beech and so there was little beech regeneration.

These dense layers of understory beech sprouts are now a conspicuous ecological feature of central Adirondacks forests, making the forests darker and the forest floors perhaps more acid than they would otherwise be.

Just how long the beech understories have been here is unknown. Beech have always been here, but is not mentioned as an understory dominant in early forestry studies.* Some of the beech understories may have developed from the selective harvesting of sugar maple and yellow birch. Others are certainly a response to the death of canopy beeches from beech-bark disease.

*For example, Pinchot (1898), Graves (1899), Hosmer and Bruce (1901, 1903), and Heimburger (1933).

BASAL AREA BY TRANSECT

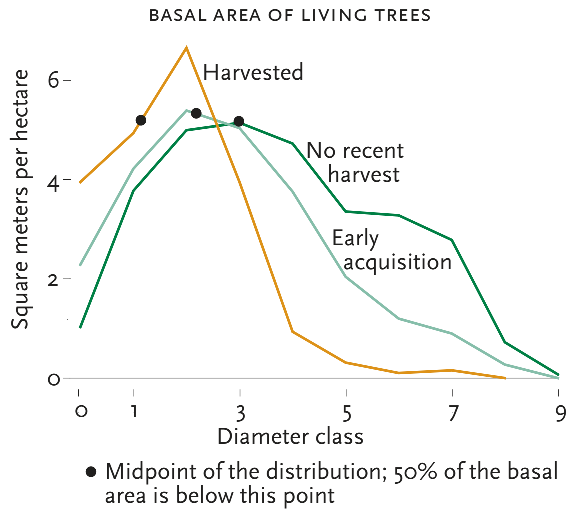


Basal Areas The basal area estimates the total amount of wood in the forest. When averaged over a transect, basal areas range from about 17 square meters per hectare (sq.m/ha) to 37 sq.m/ha, a typical range for hardwood forests in our area.

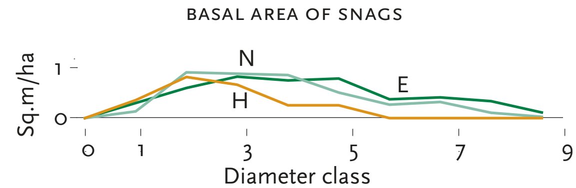
While there is considerable overlap between transects with different forest histories, particularly in the range between 25 and 30 sq.m/ha, forest history is still a reasonably good predictor of basal area. Seventy-two percent of the transects with 30 sq.m/ha of basal area or more are early acquisition, and none are harvested. Seventy-five percent of the transects with basal area less than 25 sq.m/ha are harvested, and none are early acquisition. A regression of basal area on forest history predicts 34% of the variation in basal area, and is significant at the 0.001 level.

Size Structure Most early-acquisition and no-recent-harvest forests have more big trees, both living and dead, than the recently harvested forests. Trees 50 cm in diameter are common, 80-cm trees are frequent, and 90-cm and 100-cm trees, though rare, still occur. In the early-acquisition forest 34% of the basal area is found in trees 50 cm and larger. In the no-recent-harvest forests 18% is and in the unharvested forests only 3% is.

The size distributions of the different species, shown in the graphs on p. 20, vary considerably. Sugar maples and yellow birches dominant the large-diameter class in early-acquisition and no-recent-harvest stands. Very large hemlocks are found in some stands, but not in many others. (Because we avoided dense softwoods, our sampling may underestimate the abundance of hemlock, which often occurs in pure stands.) Large red spruces occurred in many of the early acquisition stands but were never numerous. Large beeches were very rare and were never healthy. Canopy beeches are still numerous, but are mostly 30 cm or less. Many of these are young



In these plots, diameter class 0 includes trees from 0 to 9 cm dbh. Diameter class 1 includes trees from 10 to 19 cm, and so on.



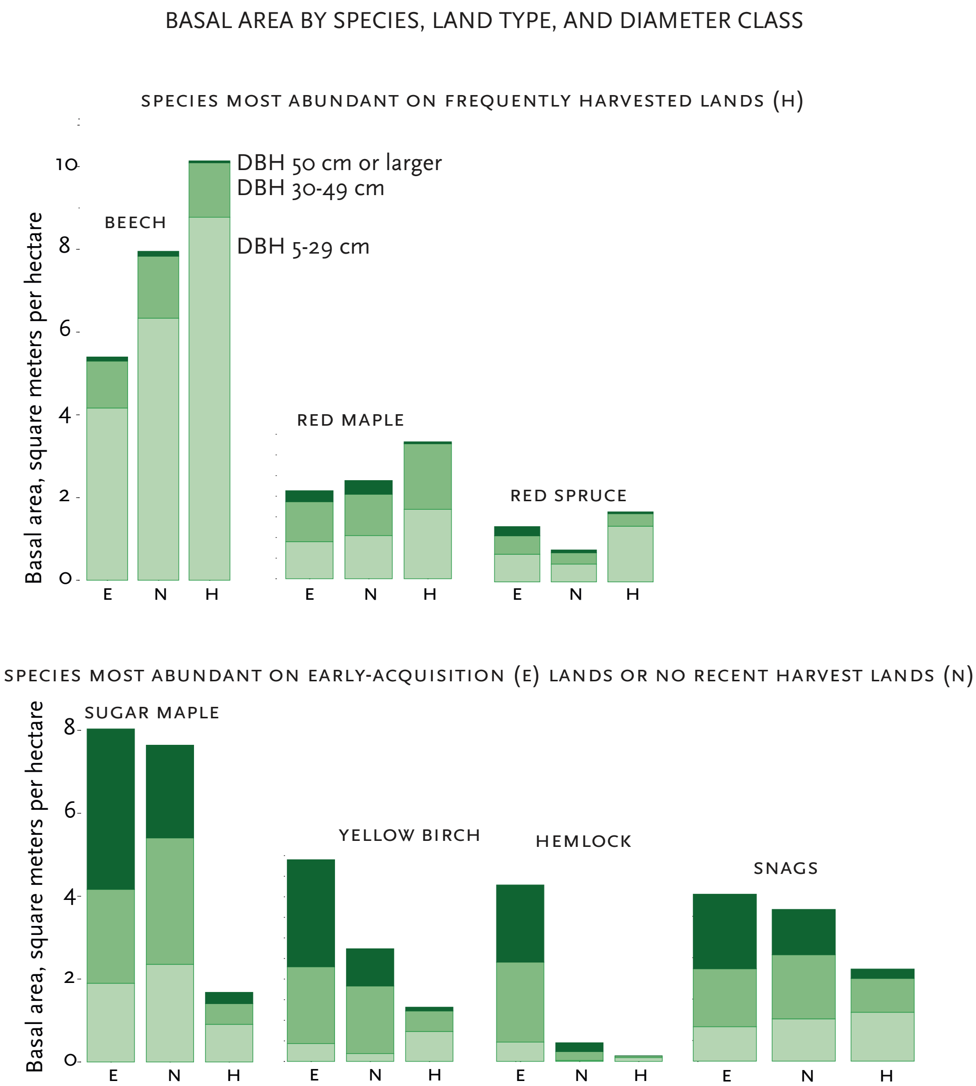
trees that sprouted or were released when the disease first started killing older trees.

The size distributions of snags (standing dead trees) in the three conditions are shown in the right-hand graph above. Because of the continuing death of medium-sized beeches, all the forests we examined have many snags in the 20 cm to 40 cm range. The older forests have many snags in the 50 cm to 80 cm range as well. The harvested forests have almost none.

The large snags are a conspicuous and unusual feature of older woods. Big living trees, while uncommon, still found throughout our area as shade and roadside trees and occasionally in the woods. Big dead trees almost never are. The big dead trees, even more than the big living ones, may be the signature of the early acquisition woods. Their natural history and role in forest processes, would be interesting to study. So far as we know, this has never been done in the Adirondacks.

We can summarize the preceding graphs by a four-variable bar graph (p. 21) that shows the amount of basal area by species, condition, and diameter class. The largest trees, living and dead, are represented by the dark green tops of the bars. Note that they are restricted, predominantly, to three species (sugar maple, yellow birch, and hemlock) and two conditions (early-acquisition and no-recent-harvest).

Understory Tree Composition Over the next century, many of the largest trees will probably



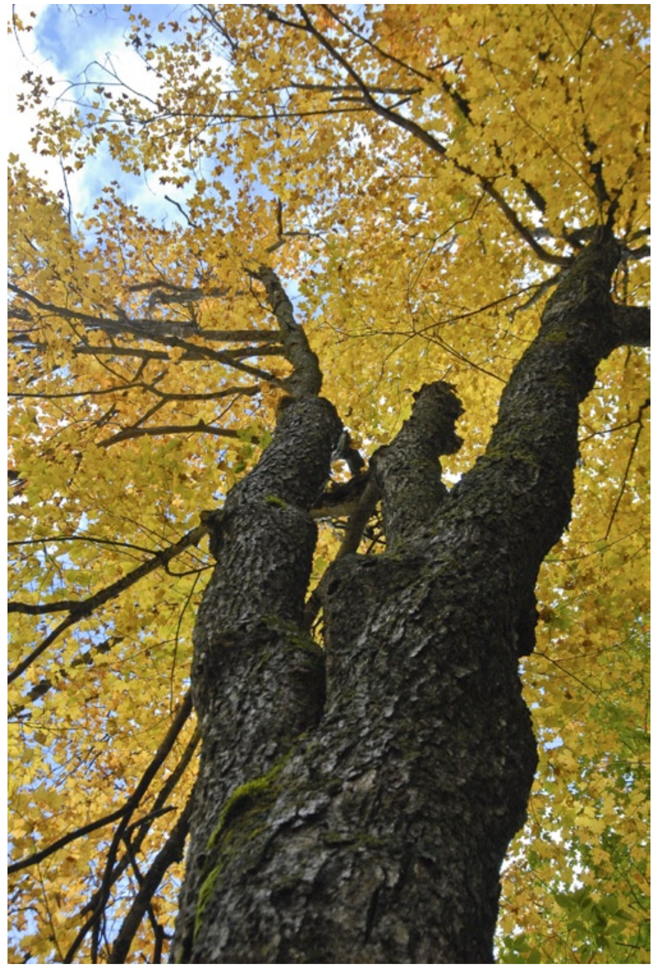
die. In some cases they will be replaced by medium-sized trees from the subcanopy, but in most cases they will be replaced by small understory trees that grow up in the gap. The composition of the future forest will thus depend on, though not duplicate, the current understory composition.

The graph on p. 24 shows the current composition of the understory, defined as all the trees under 20 cm diameter. In all forest conditions about half the understory basal area is beech. Because many of the beech are quite small, the relative number of beech stems is much higher than the relative proportion of beech basal area, but we don't have good figures for this.

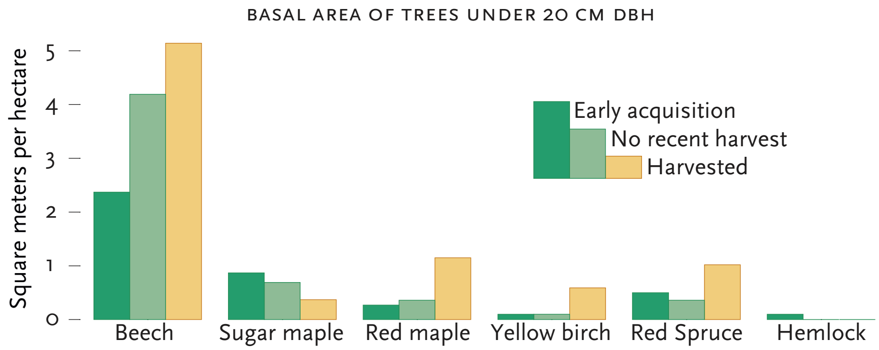
In the early-acquisition forest, there are significant amounts of understory sugar maple and red spruce. Like beech, many of the red spruces are small, and they are more numerous than their basal area suggests. In the harvested woods, there are significant amounts of red maple and red spruce and some yellow birch. But beech predominates in all cases.

Just how much these proportions will influence the woods in the next century is impossible to say. If basal area is a good predictor, the woods will remain gener-



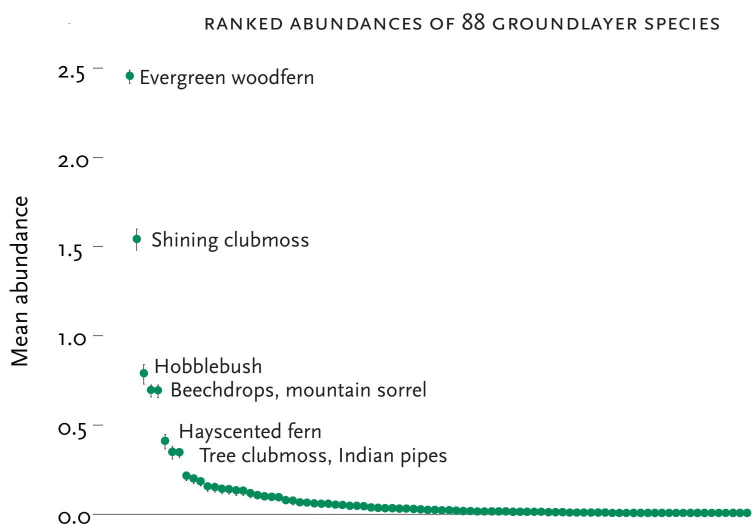
Big trees in unharvested woods. Clockwise from upper left, hemlocks north of Lower Saranac Lake; two yellow birches east of the Cedar River Flow; a large maple in a fertile cove on Water Barrel Mountain, north of the Cedar River Flow; yellow birch, beech, and spruce in early-acquisition woods in Township 40; maple forest and a large canopy maple on Water Barrel Mountain. In the second photograph, the small yellow birch on the right is about 12 inches in diameter, the typical size of harvestable trees in commercial forests.



ally mixed, though we may lose yellow birch in the old woods and sugar maple in the young ones. If the number of stems is the best predictor, beech will win hands down.

RESULTS: GROUNDLAYER COMPOSITION AND DIVERSITY

The groundlayer–the herbs and shrubs of the forest floor–was the focus of this study. We have data from 450 plots, which allow us to measure overall diversity and the abundances of individual species with moderate accuracy. The table on pp. 28-29 summarizes the data.



The abundance of a species is measured on a scale of 0 to 4, described on p. 6.

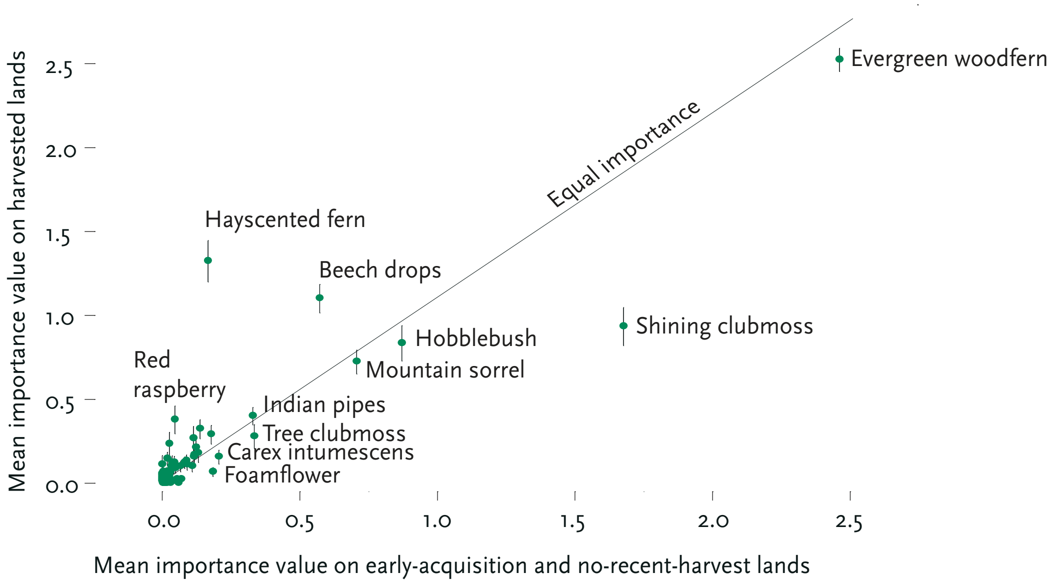
We found 88 species of herbs and shrub (not counting striped maple, which we treated as a small tree) in our plots. Another 12 species were found between plots but not in them. Because we worked in the fall, we likely missed at least two and possibly as many as four spring ephemerals. And because of the taxonomic simplifications necessary when working with sterile material (p. 7), we may have missed up to six uncommon species that resembled common ones. Thus the total upland forest flora (excluding gap species, wetland species, and roadside species) in our study areas is at least 100 species and probably not much over 110 species.

It is important to realize how small, by the standards of lower elevations and more fertile soils, this flora is, and how many common species are missing from it. We did not see, for example, hepatica, early meadow rue, white wood aster, white snakeroot, bloodroot, early saxifrage, blue-stemmed goldenrod, common pussytoes, obovate ragwort, stemmed yellow violet, false solomons-seal, or dwarf buttercup. We did not see *Carex pensylvanica, C. laxiflora, C. platyphylla, Danthonia spicata, Deschampsia flexuosa,* or *Oryzopsis asperifolia.* We did not see maple-leaved viburnum, black huckleberry, or any azaleas or shadbushes. We did see low-bush blueberry, beaked hazelnut, wild sarsaparilla, rose twisted-stalk, and jack-in-the-pulpit but all, though common elsewhere in our area, were rare in our plots.

What we did see was a group of about 15 species that occurred frequently (at 1 plot in 10 or more), and an even smaller group of 4 species that occurred at half the plots or more. These were the common species that we associate with acid mid-elevation woods. It will surprise no one who has walked in this sort of woods that the commonest species were evergreen woodfern, shining clubmoss, beechdrops, and mountain sorrel.

What was surprising was just how common this small group of species was. The average frequency of the 15 commonest species was 0.32, or 1 plot in 3. The average frequency of the 78 remaining species was 0.022, or 1 plot in 46.

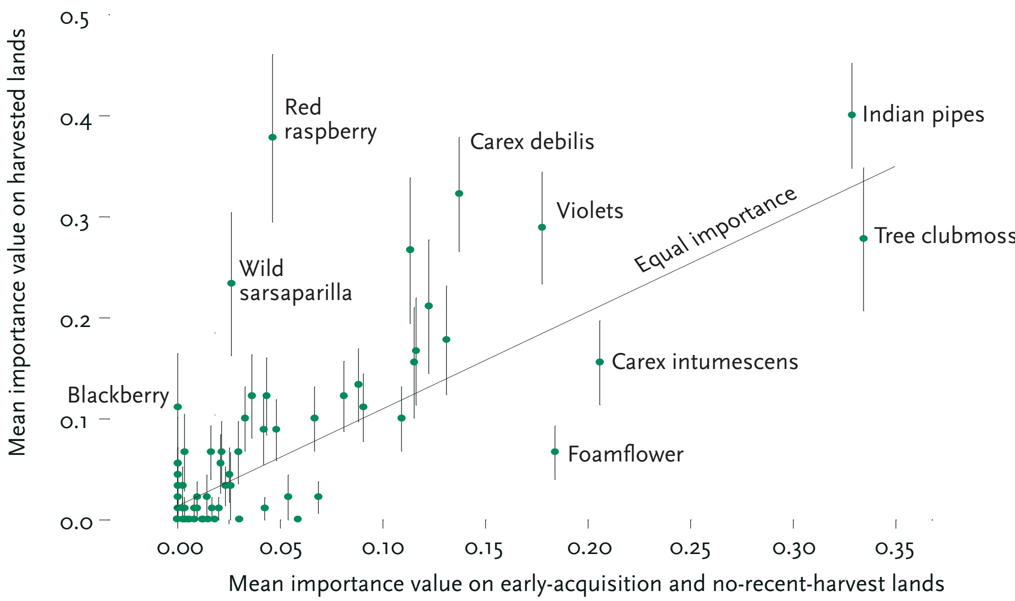
IMPORTANCE VALUES OF UNDERSTORY SPECIES ON HARVESTED AND UNHARVESTED LANDS I



Groundlayer Abundance While in the woods we looked quite carefully for evidences of species associated specifically with older woods. We found none. We saw clear changes (more clintonia, dewdrop, goldthread, dewberry, etc.) on moister sites with more conifers and we thought we saw a general depletion of understory species on transects that were heavily browsed. We also came upon three sites where we saw species (sweet cicely, silvery spleenwort, plantain-leaved sedge, baneberry, blue cohoosh…) that we associate with fertile soils. But we saw no evidence that *any* species seemed to be strongly associated with early-acquisition woods. Our overall impression was that the general floras of early-acquisition and nonrecent-harvest woods were either the same as those in harvested woods or, if anything, even simpler.

The comparative abundance data, plotted on p. 23 and with the area near the origin enlarged in the graph above, confirm this. When abundances in harvested

IMPORTANCE VALUES OF UNDERSTORY SPECIES ON HARVESTED AND UNHARVESTED LANDS II



This graph is an enlargement of the lower left-hand portion of the graph on p. 25

woods are plotted against those in unharvested woods, most species lie near the equal abundance line. A regression of abundance in harvested forests versus abundance in unharvested forests predicts 78% of the variance, and is significant at the 0.001 level.

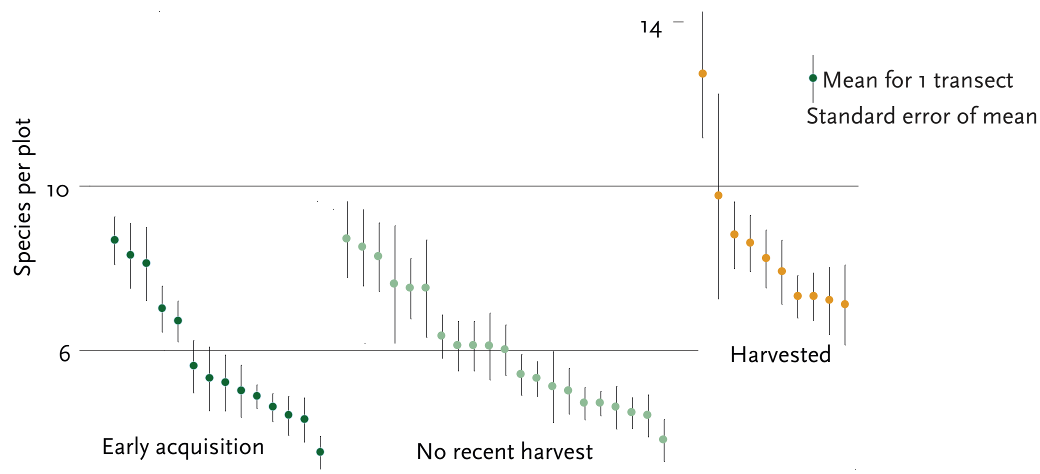
Only a few species lie more than two standard errors from the line. Red raspberry, wild sarsaparilla, stemless violets, beech drops, *Carex debilis*, and hayscented fern were significantly more common in the harvested woods. Shining clubmoss and foamflower were significantly more common in unharvested woods.

How many of the widespread groundlayer plants are forest-interior species? We would argue that there are very few if any. By our definition on p. 4 a candidate has to be reasonably widely distributed in unharvested forests, and absent or much less common in harvested ones. Candidate species, then, would occupy the lower, and especially the lower right portions of the abundance × abundance plots.

Unfortunately for the hypothesis of forest-interior species, there are only a few species in these portions of the plots. Foamflower is certainly a candidate. It is reasonably common overall and four times as common in early-acquisition woods as harvested ones, which is in its favor. But it is no more common in no-recent-harvest woods than in harvested ones, which confuses the issue. So, pending a better sense of its overall distribution, it remains only a candidate.

It is much easier to make the case that several species (hayscented fern, raspberry, blackberry, wild sarsaparilla, *Carex debilis*), at least in our dataset, favor harvested sites. This fits well with what we know of their general biology. Many species, of course, colonize disturbed sites. The only reason there are not more of them on our graphs is that we (deliberately) avoided large gaps, road edges, and areas disturbed within the last 10 or 20 years.

RANKED MEAN PLOT DIVERSITY BY TRANSECT AND CONDITION



Groundlayer Diversity Our 450 groundlayer plots ranged in diversity from two plots with only a single species to one with 18. The median was 6 species and 75% of the plots had 8 species or less. The means for the transects ranged less widely. The least diverse transect averaged 3.5 species per plot and the most diverse 12.7 species per plot. Once again the median was 6 species per plot, and the third quartile 8 species.

There are, by the standards of more diverse woods, very small numbers. Our dry woods in the Champlain Hills typically had 10 to 20 species in a 10 m × 10 m square plot, which is only 20% more area than the 5-m radius plots we used here. A high diversity, mesic forest in our area can have individual plots with 10 species in a square meter. Only 69 of our 450 plots had this many species on 79 meters.

The graph above shows the mean per-plot groundlayer diversity by transect and condition. Early-acquisition and no-recent-harvest transects have a similar range. Both often average below 6 species per plot and never average above 9 species per plot. The harvested plots, with one exception, overlap them but do not go so low; no harvested transect averaged less than 7 species per plot.

RANKED MEAN ABUNDANCES OF UNDERSTORY SPECIES

Species		Early Acquisition	No Recent Harvest	Harvested
Dryopteris intermedia	Evergreen woodfern	2.627	2.295	2.522
Lycopodium lucidulum	Shining clubmoss	1.6	1.752	0.933
Viburnum lantanoides	Hobblebush	1.46	0.281	0.833
Oxalis acetosella	Mountain sorrel	0.847	0.567	0.722
Epifagus virginiana	Beechdrops	0.487	0.657	1.1
Monotropa uniflora	Indian pipes	0.333	0.324	0.4
Tiarella cordifolia	Foamflower	0.287	0.081	0.067
Carex intumescens	Swollen sedge	0.207	0.205	0.156
Lycopodium obscurum	Tree clubmoss	0.173	0.495	0.278
Coptis trifolia	Goldthread	0.167	0.095	0.178
Lonicera canadensis	Canada honeysuckle	0.147	0.071	0.1
Thelypteris novaboracensis	New York fern	0.14	0.105	0.211
Brachyeletrum septentrionale	Harry Wood's grass	0.113	0.119	0.167
Rubus pubescens	Dwarf blackberry	0.113	0.024	0.022
Mitchella repens	Partridgeberry	0.1	0.081	0.111
Trientalis borealis	Starflower	0.1	0.076	0.133
Dennstaedia punctilobula	Hay-scented fern	0.1	0.233	1.322
Polystichum acrostichoides	Christmas fern	0.093	0.024	0
Viola sp.	Violet	0.093	0.262	0.289
Carex debilis		0.093	0.181	0.322
Cornus canadensis	Bunchberry	0.08	0.005	0.011
Lycopodium annotinum	Stiff clubmoss	0.073	0.157	0.156
Cinna latifolia	Wood reed	0.067	0.067	0.1
Medeola virginiana	Wild cucumber	0.067	0.095	0.122
Corylus cornuta	Beaked hazelnut	0.06	0	0
Uvularia sessilifolia	Bellwort	0.06	0.048	0.022
Viola rotundifolia	Early yellow violet	0.06	0.167	0.267
Dalibarda repens	Dewdrop	0.047	0.005	0.033
Rubus idaeus	Red raspberry	0.04	0.052	0.378
Maianthemum canadensis	Canada maiflower	0.027	0.01	0.144
Cornus alterniflora	Alternate dogwood	0.027	0.01	0
Carex novae-angliae	New England sedge	0.027	0.024	0.044
Carex leptonervia	Few-nerved sedge	0.027	0.057	0.089
Clintonia borealis	Clintonia	0.02	0.01	0
Gymnocarpium dryopteris	Oak fern	0.02	0.005	0
Trillium undulatum	Painted Trillium	0.02	0.076	0.089
Aster acuminatus	Acuminate aster	0.02	0.052	0.122
Carex communis	Common sedge	0.02	0.067	0.122
Galium triflorum	Three-flowered bedstraw	0.013	0.019	0.067
Polygonatum pubescens	Solomon's seal	0.013	0.033	0.033
Carex brunnescens		0.013	0.052	0.1
Rubus canadensis	Canada blackberry	0.013	0.029	0.056
Galium sp.	Bedstraw	0.007	0	0
Glyceria striata	Striate manna grass	0.007	0	0
Pyrola secunda	One-sided shinleaf	0.007	0	0
Dentaria diphylla	Toothwort	0.007	0	0
Osmunda cinnamomea	Cinnamon fern	0.007	0	0.067
Osmunda claytonii	Interupted Fern	0.007	0	0.011
Solidage flexicaulis	Zig-zag goldenrod	0.007	0.01	0
Phegopteris connectilis	Narrow beech fern	0.007	0.01	0.011
Trillium erectum	Red trillium	0.007	0.052	0.067
Viburnum cassinoides	Wild raisin	0.007	0.005	0
Carex sp.		0.007	0.033	0.011
Streptopus roseus	Rose twisted-stalk	0	0	0.033

Sorbus americana	American mountain-ash	0	0	0.011	
Rubus alleghaniensis	Allegheny blackberry	0	0	0.111	
Pteridium aquilinum	Bracken	0	0	0.056	
Polygonum ciliare	Ciliate bindweed	0	0	0.033	
Epipactis helleborine	Helleborine	0	0	0.011	
Aster umbellatus	Umbellate aster	0	0	0.011	
Agrostis perennis		0	0	0.011	
Cypripedium acaule	Pink lady-slipper	0	0	0.044	
Botrychium dissectum	Cut-leaved grapefern	0	0	0.022	
Solidago rugosa	Rough-stemmed goldenrod		0	0	0.044
Lycopodium clavatum	Staghorn clubmoss	0	0	0.011	
Carex from Ovales		0	0	0.011	
Potentilla simplex	Common cinquefoil	0	0	0.011	
Carex gynandra		0	0	0.022	
Taxus canadensis	Canada yew	0	0.005	0	
Carex disperma	Two-seeded sedge	0	0.005	0	
Carex deweyana	Dewey's sedge	0	0.005	0	
Vaccinium angustifolium	Early lowbush blueberry	0	0.005	0.011	
Aralia nudicaulis	Wild sarsaparilla	0	0.052	0.233	
Dryopteris marginalis	Marginal woodfern	0	0.005	0	
Polypodium virginianum	Common polypody	0	0.024	0	
Laportea canadensis	Wood nettle	0	0.01	0	
Actea pachypoda	White baneberry	0	0.005	0	
Osmorhiza claytoniana	Sweet cicely	0	0.005	0	
Arisaema triphyllum	Jack-in-the-pulpit	0	0.019	0.011	
Pyrola sp.	Shinleaf	0	0.005	0	
Dryopteris campyloptera	Mountain woodfern	0	0.024	0	
Glyceria sp.	Manna grass	0	0.005	0	
Athyrium felix-femina	Lady fern	0	0.019	0.022	
Danthonia compressa		0	0.005	0.033	
Lycopodium digitatum	Ground cedar	0	0.029	0.022	
Platanthera orbiculata	Large-leaved orchid	0	0.005	0	
Sambucus pubens	Red elderberry	0	0.043	0.067	
Prenanthes altissima	Wild white lettuce	0	0.033	0.011	

Additional species, not in plots

Adiantum pedatum	Maidenhair fern
Aralia racemosa	Spikenard
Aster macrophyllus	Large-leaved aster
Botrychium virginianum	Rattlesnake fern
Caulophyllum thalictroides	Blue cohoosh
Carex plantaginea	Plantain-leaved sedge
Depraria acrostichoides	Silvery spleenwort
Impatiens capensis	Orange jewel-weed
Millium effusum	Wild millet
Ribes lacustre	Swamp currant
Tilia americana	Basswood
Viola canadensis	Canada violet

How much might the ephemeral and early senescing species effect these results? We won't know until we have better data, but the numbers that we do have suggest that they don't contribute much to overall diversity, and that they are as common or commoner in harvested woods than in unharvested ones.

The six species for which we have the clearest evidence of early senescence (p. 8) are red trillium, painted trillium, cucumber root, bellwort, clintonia, and starflower. Taken together, they contributed 0.4 species per plot to the average diversity, meaning that one of them was found in every 2.5 plots. Before October 15, the time when most of them senesced, they contributed a total of 0.7 species per plot. It is reasonable to suppose that if we had sampled them earlier they might have averaged 0.7 species per plot throughout the survey, raising the average diversity by 0.3 species per plot. This is less than the standard error of our transect estimates, and clearly would not affect any of our conclusions.

If we look at the average abundance of these species in harvested and unharvested lands, restricting ourselves to that records from before October 15, we find that five of the six are slightly more common in harvested lands than in unharvested lands, and one (bellwort) is slightly rarer. Their abundances are all low and hence uncertain. All we can really say is that, using the admittedly incomplete data that we currently have, none looks like a good candidate for a forest-interior species.

What controls diversity? Clearly disturbance and perhaps deer, but beyond that we do not know.

The case for disturbance is straightforward but, since we didn't sample open or recently disturbed areas, is not quantitative. Nonetheless, it was easy to see in the field (and consistent with a large literature) that persistently open and recently disturbed areas had a lot of species that forest interiors didn't.

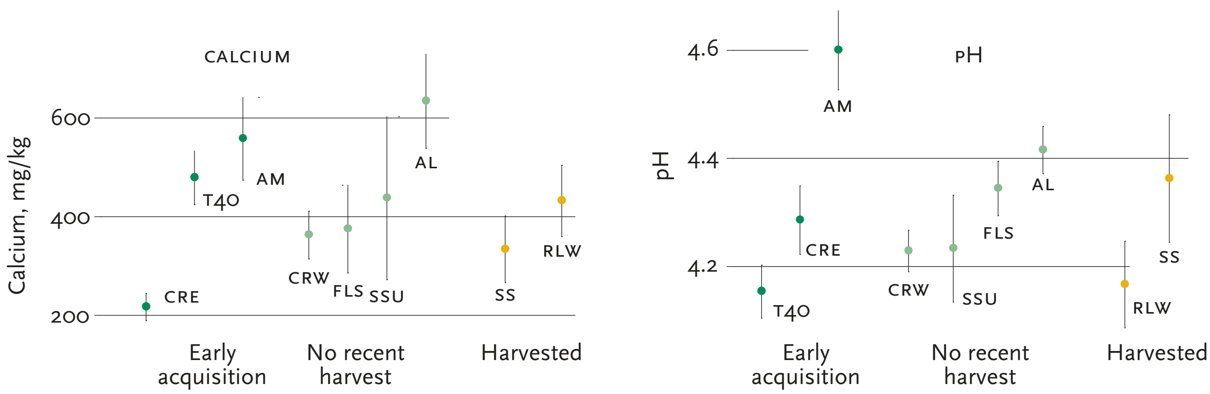
The case for the effects of deer is weaker but still interesting. In general, though deer sign was widespread, heavy winter browsing was uncommon. But where we did see it, the abundance and diversity of the groundlayer species were often conspicuously reduced.

The most striking example was on transect LB1. This was an early-acquisition forest northeast of Ampersand Mountain with many big trees and a dense understory of small beech. The beech had been heavily browsed, and there was a clear browse line at about 1.5 meters: if you stood up, your head was in a layer of beech leaves and branches. If you bent down, you could see for a hundred meters or so, with almost nothing in you way.

The groundlayer on this transect was strikingly depauperate. The mean diversity was 3.5 species per plot, the lowest we observed in our study, and roughly half that of less browsed plots nearby on Ampersand Mountain. The average abundance of evergreen woodfern, the most abundant species on the transect, was only 0.3, compared to 2.45 for the study as a whole. Shining clubmoss and hobblebush, the second and third most abundant species in the study as a whole (mean abundances 1.5 and 0.8) were both completely absent.

Beyond harvesting (good for diversity) and deer (bad in large numbers) we have no clear leads. We found no useful correlations between any of our other variables (slope, aspect, canopy cover, subcanopy cover, pH, soil organic mater, cation exchange capacity, soil nutrients…) and diversity.

SOIL CHEMISTRY BY SITE



CRE	Cedar River Flow East	CRW	Cedar river Flow West	AL	Ampersand Lake
T40	Township 40	FLS	Forked lake South	SS	Shingle Shanty, harvested
AM	Ampersand Mountain	SSU	Shingle Shanty, unharvested	RLW	Round Lake and Whitney

Chemistry, History, and the Groundlayer There are general reasons for believing that harvesting, which removes nutrients, will affect soil chemistry, and that soil chemistry, which supplies the nutrients for plant growth, will affect the composition of the groundlayer. But our study affords no evidence of either effect.

When we compared the soil chemistry of different sites, as shown for calcium and pH above, we found a broad overlap between sites of different histories, and no evidence of consistent differences.

When we looked at the (few) plots where we saw species believed to indicate fertile soils, we did not find exceptional soil chemistries

Plots	Number of fertility indicators	Nearest soil plots	pH	Calcium, mg/kg
103, 104 111	6	101, 110	4.3, 4.4	230, 451
336	6	336	4.5	819
340	2	341	5.0	753
Cove	7	Cove	4.7	3.77

And likewise, where we found exceptional soil chemistry, we usually found few or no fertility indicators:

Plots	Number of fertility indicators	pH	Calcium, mg/kg
56	0	4.3	1198
286	0	4.6	972
341	1	5.0	753
351	0	4.8	128
401	0	4.4	970
441	0	4.8	766

The data suggest a weak association between indicators, pH, and calcium around plots 336, 340, and 341. Otherwise no association appears.

This must not be taken as a general result. We saw very few indicator species in the whole study, and so this is a poor data set to use to investigate their occurrence.

All that can really be said is that fertility indicators are rare in central Adirondack forests, and we have no idea whether their occurrence is fortuitous or controlled by the environment.

RESULTS: BRYOPHYTE SUBSTRATES, FREQUENCIES, AND COVER

The bryophyte part of this study consisted of lists of dominant species and estimates of the amount of substrate and proportion of this substrate covered by bryophytes on 100 plots.

Before we give the results there are two caveats. We remind you that the work was hasty and sometimes done under poor observing conditions, and the results are correspondingly crude. And we note that our 100 bryophyte plots contain a total of 5,000 square meters–1/2 hectare–for all three forest conditions. Hence that they will not adequately sample habitats that occur with a frequency of less than about 10 per hectare in any conditions. Several of the interesting bryophyte habitats–the bases of large trees and snags, large diameter logs–occurred at frequencies this low and lower, and were correspondingly poorly sampled.

Thus while we had many trees with basal diameters of 70 cm in our prism plots, we only sampled 17 in the moss plots. Likewise, while we saw logs up to 60 cm in diameter and 15 meters long in the early-acquisition forests, no log wider than 30 cm or longer than 4 meters occurred in the our samples. There is thus much interesting habitat in the woods that didn't get into our plots, and we would need a different study design–perhaps variable-radius plots or belt transects–to sample it.

Dominant Species As with the vascular plants, the bryoflora of these woods is dominated by a few very common species. The most abundant are:

Hypnum imponens, mostly on logs, and *H. pallescens* on logs and rocks.

Dicranum scoparium, *fulvum,* and perhaps *flagellare* on tree bases and rocks, *D. montanum* on bark and logs, and *D. viride* and *flagellare* on logs.

Brachythecium salebrosum, oxyxladon, reflexum and several other less common species on tree bases and logs.

Mnium ciliare and *Plagiomnium cuspidatum* on tree bases, moist rocks and logs.

Callicladium haldanium on logs and tree bases.

Thuidium delicatulum on low moist rocks.

Brotherella recurvans on moist rocks and well-decayed logs.

The liverworts *Nowellia curvirostre, Lophocolea heterophylla* and *Ptilidium pulcherrimum* on logs that have lost their bark are just starting to rot.

Platygyrium repens, Ulota americana, and *Porella platyphylla* on the bark of living trees and sometimes on newly fallen logs.

Neckera pennata and *porella platyphylla* on the trunks of large trees, especially sugar maples, and *Anomodon attenuatus* at their bases.

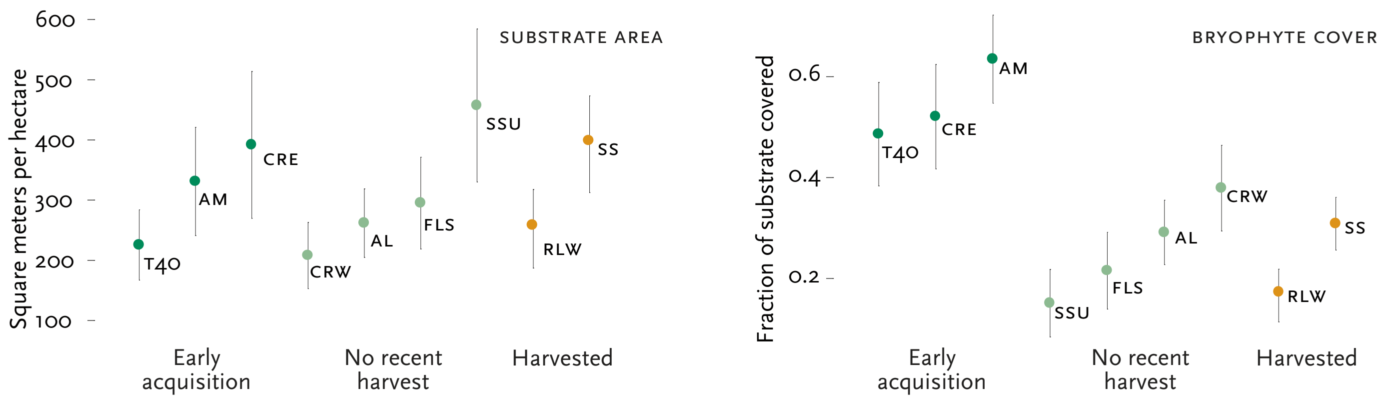
Polytrichum pallidisetum and perhaps other species on soil.

Several species of *Plagiothecium, Isopterygium,* and their relatives on moist tree bases and the lower sides of rocks.

Paraleucobryum longifolium casually on dry rocks.

As with the vascular plants, this list is noteworthy for what is not on it. There were few or no grimmias, schistidiums, andraeas, orthotrichums, or needle-tipped polytrichums, all common groups in dryer or rockier woods. The characteristic species of conifer woods–*Hylocomium splendens, Bazzania tridentata, Dicranum polysetum, Ptilium crista-castrense,* and *Pleurozium schreberi*–were largely absent from upland hardwood stands, though they appeared immediately when we got into moist conifer woods. And even such common moist woods species as *Leucobryum glaucum, Herzogiella striatella, Climacium americanum, Fissidens dubius,* and *Atrichum altecristatum* were rare or absent here.

BRYOPHYTES ON LOGS

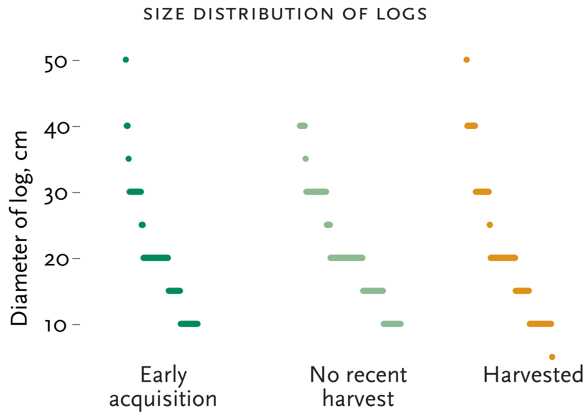


For the site codes in the graph, see p. 31.

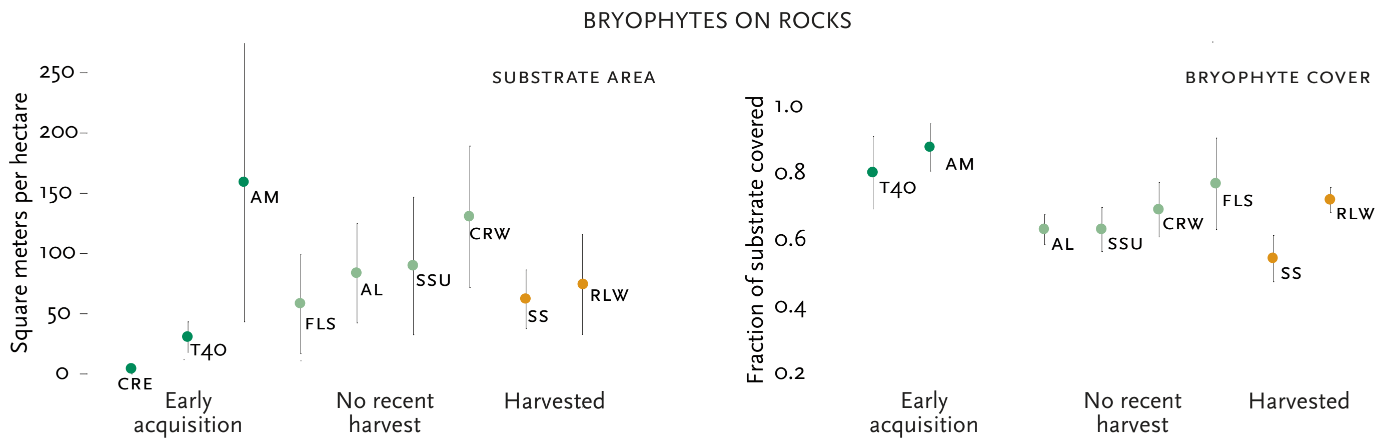
amount of Various Substrates Our sampling yielded estimates of the area of rocks, logs, stumps, and tree bases and the proportions of each covered by bryophytes. Because we had only two bryophyte plots per transect, we averaged all the transects at a site and report the averages for each site. The results for logs are shown above.

The average area of logs (summing over all the stages of decay) was about the same in all three forest conditions. The cover was not. It was similar in harvested and no-recent-harvest plots, but distinctly higher in early acquisition plots.

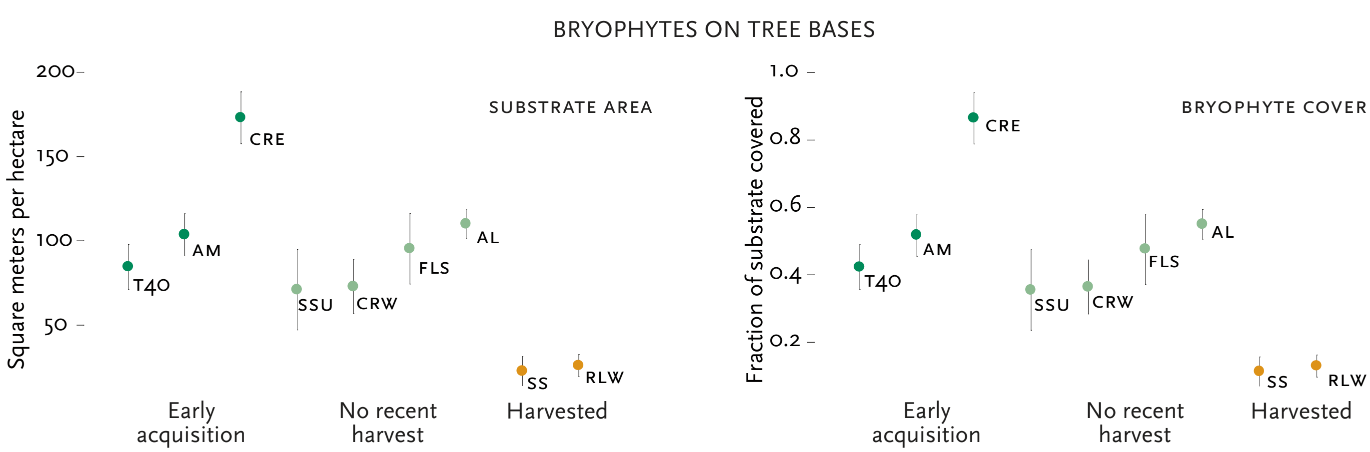
It may seem odd that woods with big trees have the same amount of logs as woods with small ones. There are probably two reasons for this: first, the big trees are relatively rare, and, second, beech-bark disease has killed large number of medium-sized trees, many of which have fallen and are now logs. For both these reasons, the commonest diameters for both snags (graph on p. 20) and logs (graph on p. 34) are 20 cm to 40 cm.

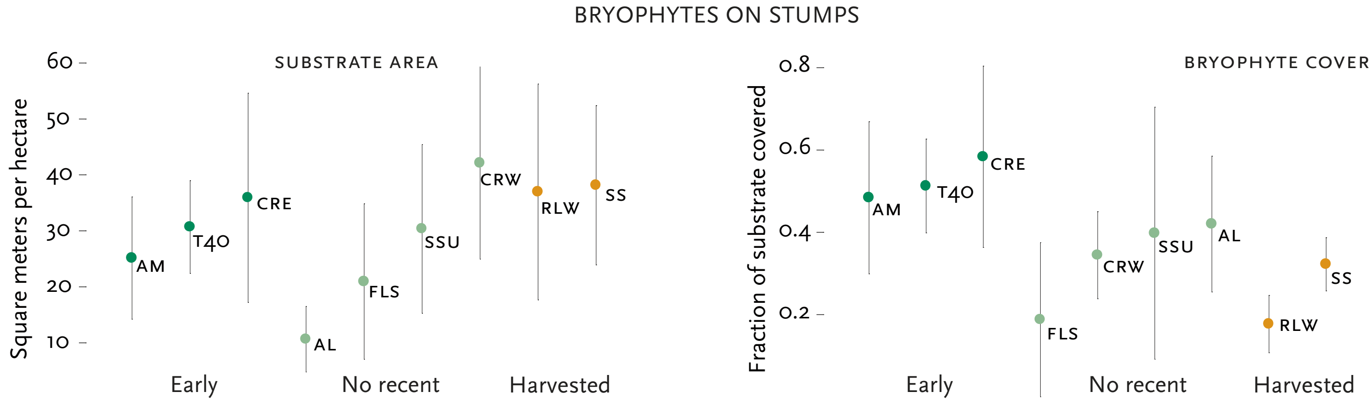


Rocks, shown in the graph below, are less abundant than logs but have more cover. They have only about a third the total area of the logs, but twice the average cover. The differences between the different forest histories are small: the means for the early-acquisition sites are higher than those of the no-recent-harvest and harvested ones, but the differences are not very strong.



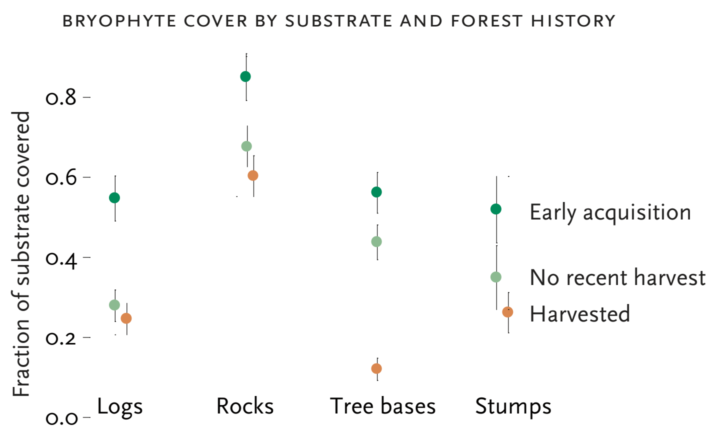
Tree bases, shown below, are comparable to rocks in their area and to logs in their cover. Here there are strong differences between unharvested and harvested sites. The unharvested ones have both much more area and a much higher cover than the harvested ones. The no-recent-harvest sites are intermediate.





Stumps are the rarest bryophyte habitats, and so are the ones about which we have the lowest statistical certainty. They appear to be marginally more abundant in harvested woods than unharvested ones and somewhat better covered in early-acquisition sites than either harvested or no-recent-harvest ones. But the standard errors are large and the conclusions weak.

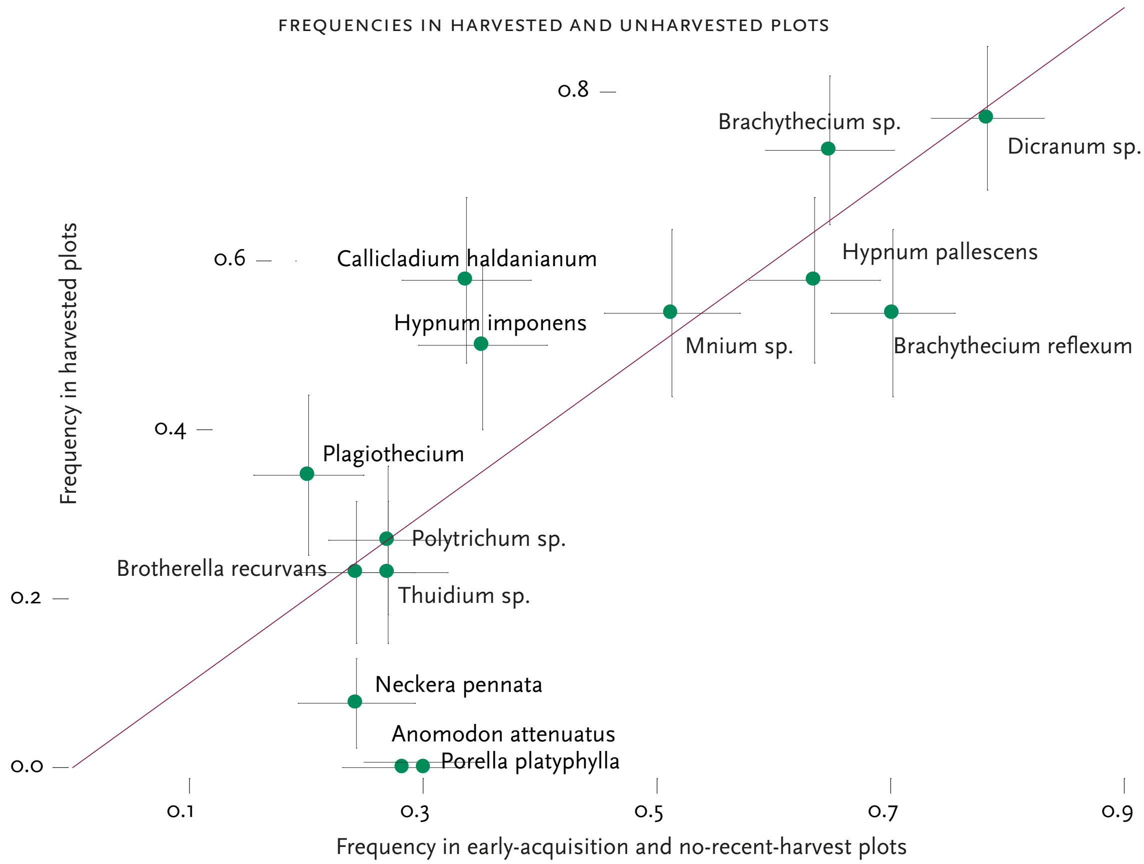
The graph below sums up the cover data. There appear to be clear differences in the cover of early-acquisition and harvested bryophytes on all 4 substrates and between no-recent-harvest and harvested bryophytes on tree bases. In all these instances, the cover on the substrates in harvested forests is less.



Are there forest-interior bryophytes in central Adirondack hardwood forests? Given the crudeness of our surveys we can at most make a weak statement. From the graph on p. 36, using the same principles we used for vascular plants on p. 25, none of the common species of rocks, logs, or stumps appear to be forest-interior species. But three species of tree trunks and tree bases, *Neckera pennata*, *Porella platyphylla* and *Anomodon attenuatus*, are significantly commoner in unharvested plots than harvested ones and appear to be forest-interior species.

The natural history of these species is interesting and in some cases puzzling.* Neckera occurs almost entirely on the trunks of living trees. It is most common x found on large trees, especially but not exclusively sugar males, though it will grow well on smaller trees when transplanted to them. It is most often found in unharvested woods, but it is not clear whether this is because there is something special

*For the natural history and occurrence of *Neckera* see McGee and Kimmerer (2002, 2004), and Shluter and Reed, (2001). McGee and Kimmerer (2002) also discuss *Anomodon* and *Porella*.



about the woods, or simply because the big trees that *Neckera* likes to grow on are commoner there.

Neckera has a distinctive growth form, adapted to intercepting and retaining water and nutrients running down the trunks of trees. It makes broad shaggy fringes or collars that extend out from the trunk. *Leucodon brachypus* and *Porella* do the same, but the *Neckera* fringes, when well developed, are larger than either of those.

The lichen *Lobaria pulmonaria* has a similar fringing growth habit and a similar preference for large old maples. It is less common than *Neckera;* you often find *Neckera* without *Lobaria* but rarely *Lobaria* without *Neckera.*

Anomodon attenuatus and *Porella platyphylla* are more common overall than *Neckera* but have similarly sharp ecological boundaries. Both are standard species of mesic calcareous boulders and ledges and can be extremely abundant in areas like the Taconic Mountains and western Green Mountains where the bedrock is limy. They also occurs on tree bases, and, in areas like the central Adirondacks where the bedrock is acid, seems to be restricted to them.

Anomodon also has a distinctive growth form, which, like *Neckera*, is adapted both to intercepting and retaining water. It makes thick, loose, stockings that cover the base of the tree and can be up to 5 cm deep and extend as much as two meters up the trunk. Other tree base species, particularly *Brachythecium oxycladon* and *B. salebrosum,* make basal mats or stockings as well, but they are rarely as high and never as deep.

Stockings of *Anomodon attenuatus* and *Porella platyphylla* on a sugar maple base, with *Neckera pennata* on the bole

An *Anomodon attenuatus* mat

Neckera pennata fringes on a sugar maple

Lobaria pulmonaria on a sugar maple

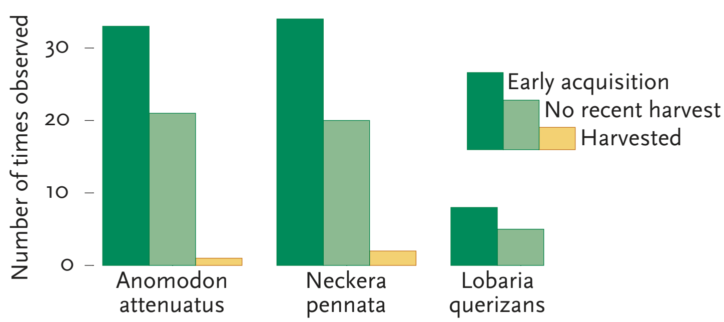
The same tree from the side

We saw both *Porella* and *Anomodon attenuatus* frequently on tree bases in our survey, but found them to be fairly choosy: they were most common on the bases of large sugar maples in moist woods, and much less common on smaller maples and other species of all sizes.

All three species–*Neckera, Porella, Anomodon attenuatus*–were strongly associated with large trees in our study. Since almost all the large trees are on the early-acquisition and no-recent-harvest lands, they fit our definition of forest interior species. Thus we concur with the conclusion of McGee and Kimmerer (2002) that in the central Adirondacks these species are largely restricted to old growth.

McGee and Kimmerer also mention *Brachythecium oxycladon, Anomodon rugelii,* and *Leucodon brachypus* as species that are associated with large trees. We believe them but don't have the data to confirm their results. We could not separate *B. oxycladon* reliably in the field from several of its more weedy relatives; we looked for *A. rugelii* but had relatively few of the big maples it likes in our plots and did not find it; and we saw *Leucodon* on big maples but above the height where our sampling stopped.

OBSERVATIONS OF ANOMODON, NECKERA, AND LOBARIA



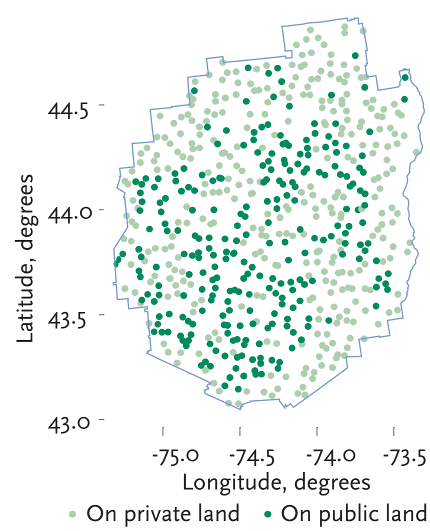
These observations include both plants seem in our plots and plants seen between them.

The *Neckera* fringes and *Anomodon* stockings are distinctive biological features of trees with large crowns and presumably much stem flow, and are best developed on large old trees. We came to think of them, along with the big snags, as one of distinctive biological signatures of unharvested Adirondack forests.

Because big trees were uncommon in our plots, we kept a tally of how many we saw *Neckera* and *Anomodon* on trees near or between plots. The results are not exact because we were not searching a known area, but they are interesting none the less, and strongly support the hypothesis that these are forest-interior species.

We saw *Anomodon* and *Neckera* were seen a total of 108 times in unharvested woods and 3 times in harvested woods. *Lobaria* was seen 13 times in unharvested woods and never seen in harvested ones. Thus if we want strong candidates for forest-interior species, and if we want, for conservation purposes, them to be moderate sized, widely distributed, and easily recognizable, these three are among the best we have.

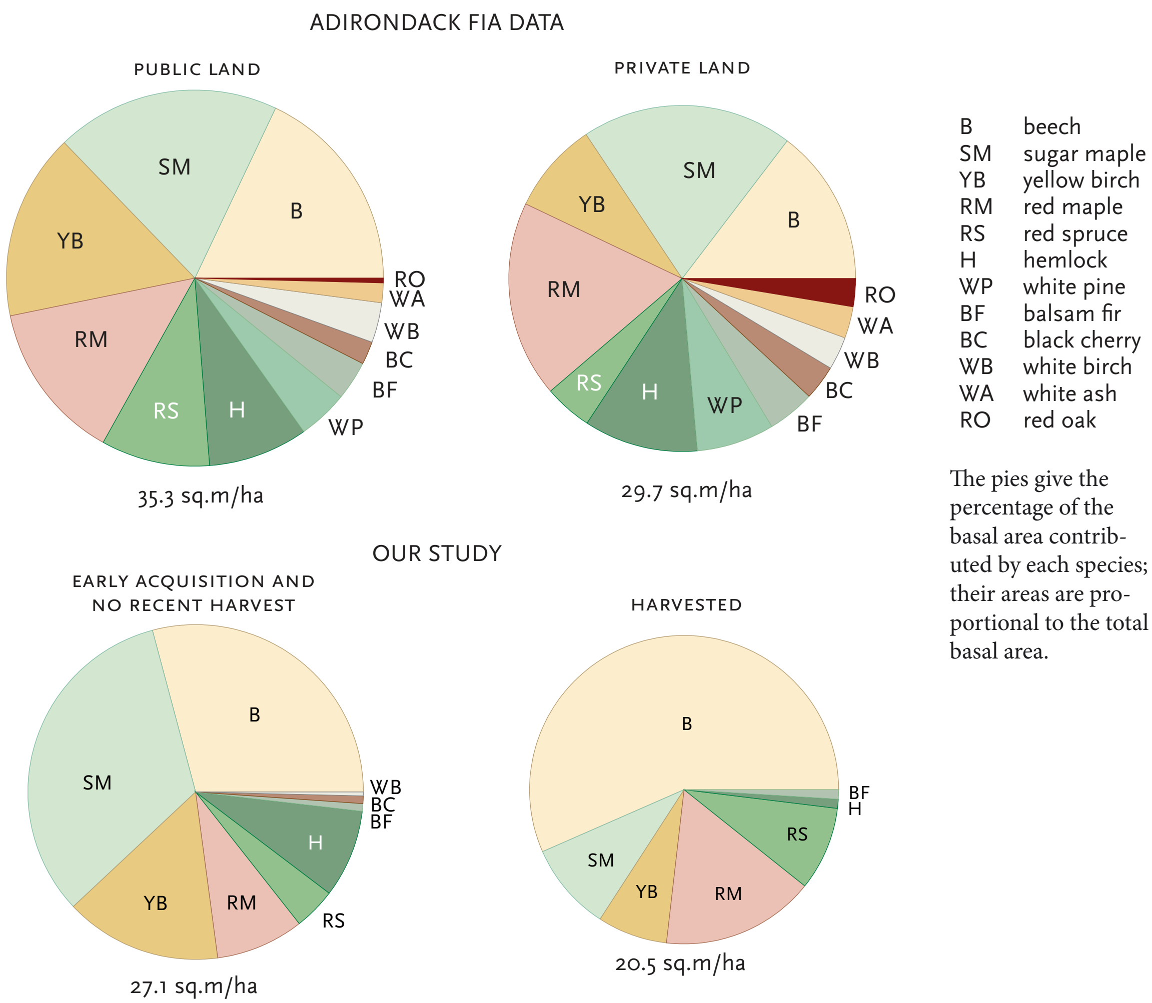
ADIRONDACK FIA PLOTS FROM HARDWOODS



Our data were gathered from 8 sites in one part of the Adirondacks. How representative are they of the park as a whole? Do our findings about the differences between harvested and unharvested hold elsewhere in the Adirondacks?

We can answer this question for trees by using data from the U.S. Forest Service Forest Inventory and Analysis Program (FIA). The FIA gathers data from permanent plots on public and private lands. At each plot, trees 12.5 cm in diameter and over are counted on four subplots totaling 1/15 hectare, and trees from 2.5 to 12.5 cm on four subplots totaling 1/186 hectare.

Charlie Canham and Nicole Rogers have created a dataset of 586 Adirondack FIA plots from hardwood forests, which we use here. The approximate locations of the plots are shown on p. 38; the Forest Service doesn't disclose the exact locations. This prevents us from separating out the early-acquisition and no-recent-harvest plots. The best we can do is separate the plots by ownership.



The pies give the percentage of the basal area contributed by each species; their areas are proportional to the total basal area.

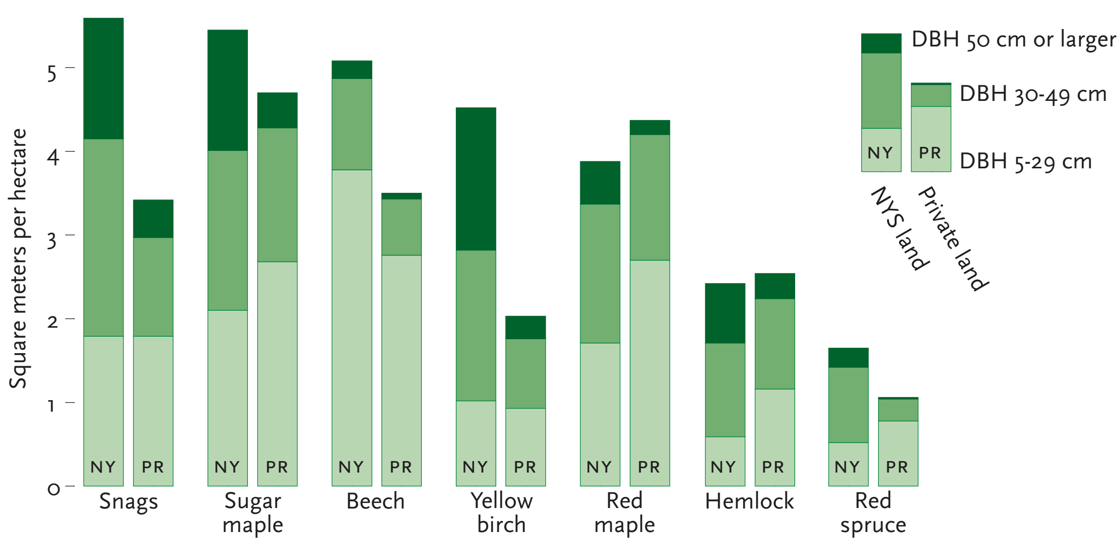
The pies shown the overall forest composition of the FIA plots and our plots. In comparing them, note that the FIA public lands (New York State Forest Preserve) correspond fairly closely to our early-acquisition and no-recent-harvest lands. The major differences are a few properties like Whitney that have had recent harvests but are now public lands. The FIA private lands, however, contain many properties that have not had recent harvests, and so are actually closer to our no-recent-harvest lands than our harvested lands.

With these differences noted, the two left graphs (FIA public lands and our early-acquisition and no-recent-harvest) are fairly similar. The main difference is that the FIA plots have more low elevation species (white ash, red oak, black cherry) and disturbance species (white pine, balsam fir, white birch). Given that our plots were at middle elevations and we avoided areas that had major historical disturbances, this all makes sense.

The right graphs on p. 39 (FIA private lands and our harvested lands) are much more different. We saw many forests dominated by young beech. They saw more mixed forests, with other successional species.

Again this seems reasonable, given the differences in sampling. We were looking at lands that had started with a significant amount of beech, been hard hit by the beech-bark disease, and then had been harvested, releasing the beech sprouts. Many of the private lands in the FIA sample had less beech to start with and have not been harvested since the peak of the beech disease.

BASAL AREA BY DIAMETER CLASS, ADIRONDACK FIA DATA



By binning the FIA data by diameter, we can get a graph of the diameter distribution by species and ownership, comparable to our graph on p. 21. The major patterns are very comparable to those in our data: the largest trees are sugar maples, yellow birches and hemlocks, and predominantly found on state land.

COMPARISONS: TOWNSHIP 40 IN 1900 AND THE GROUNDLAYER IN 1930

Since the late 1800s, when the state began to acquire lands for the Forest Preserve, Adirondack forests have seen storms, fire, harvesting, climate warming, acid deposition, and important outbreaks of pests and diseases. Thus the early-acquisition forests we see today are certainly not the forests we would have seen in 1900. It would be fascinating to be able to determine how they have changed.

Our data afford several opportunities to do this. We report on two of them here.

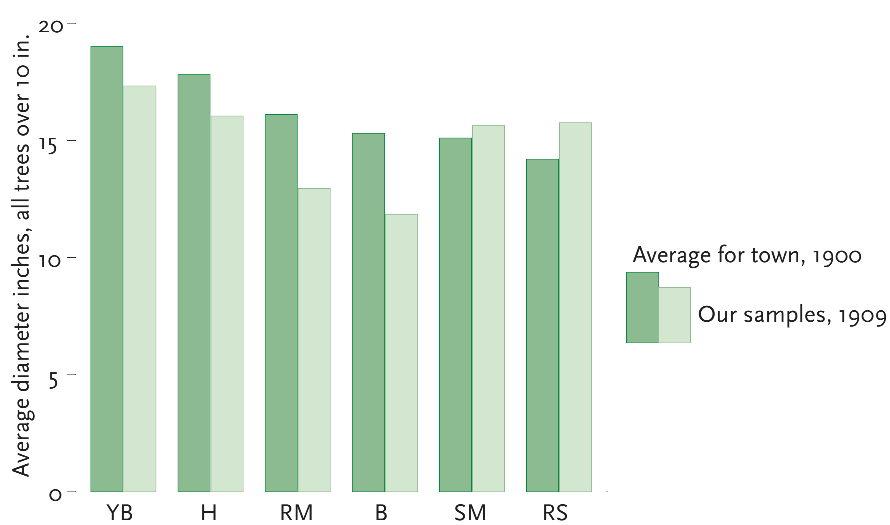
The first uses forest inventory data gathered in 1900 by Ralph Hosmer and Eugene Bruce of the U.S. Department of Agriculture. They were sent to the Adirondacks by Gifford Pinchot, who had been heading the USDA's Division of Forestry since 1898. Pinchot was anxious to demonstrate the value of scientific forest mensuration and forest planning, and also to spar with the conservationists who wished to leave virgin timber unharvested. The central Adirondacks, where New York State owned large amounts of timber, offered opportunities for both. He and his staff published several reports on the potential value of the New York's Adirondack land, complete with cutting plans, dams, mills, and railroads. The fact that the state constitution explicitly prevented any of this was conceded by the plans, but only as an obstacle, like steep terrain or an unnavigable river, that would need to be overcome if scientific forestry was to prevail.

The Hosmer and Bruce data were gathered from Township 40, surrounding Raquette Lake. Their work was requested, and partly paid for, by the New York Forest, Fish, and Game Commission, which was attempting (as it would for many years) to overturn the constitutional ban on logging in the Forest Preserve.

Hosmer and Bruce have a series of tables that give the number of trees over 10 inches in diameter in different forest types. The commonest forest type in their study, covering 88% of the township, was what they called "spruce lands" and we would call mixed upland forests. They say that red spruce was by far the commonest tree in these forests, making 46% of all the stems over 10 inches in diameter.

We did 6 transect in the northern part of Township 40, and measured tree diameters in 12 plots. The next two graphs compare Hosmer and Bruce's figures for the average diameter and density of trees on the spruce lands to ours.

APPARENT CHANGES IN AVERAGE DIAMETER ON "SPRUCE LANDS" IN TOWNSHIP 40



apparent changes in tree abundance on the "spruce lands" in township 40

When we compare average diameters, as in the graph on p. 41, our forests and theirs look very similar. Red maple and beech are a bit smaller in our plots, the others mostly the same.

When we plot numbers of trees, as in the graph above, the forests look very different. We show comparable quantities of beech and sugar maple, more red maple, and less red spruce, yellow birch, and hemlock. The change in red spruce has been particularly striking. In 1900 there were 24 over 10 inches stems per acre; now there are 0.8.

We need to stress that our sample is small. But still the pictures is broadly consistent and fits our field observations. At least four sources report between 30% and 50% spruce in mid-elevation Adirondack upland forests around 1900*. Currently we simply don't see this. We see spruce in the swamps and on the flats and upper slopes. But we rarely if ever see a hardwood forest with over 10% spruce at middle elevations.

* Fox (1895), Pinchot (1898), and Hosmer and Bruce (1901, 1903).

Township 40 has been in the Forest Preserve since the early 1890s and as far as anyone knows, it has never been harvested and has had no major fires or blowdown. If it has in fact lost 97% of its large spruce in the last century, it has done it cryptically, without major disturbance. To those of us who are trying to think about forest dynamics in the coming century, this is both interesting and cautionary.

The Groundlayer Plants in 1930 One reason we might not be finding forest interior species is that there are none. Another might be that they were once here and have been eliminated by ecological change. We have plenty of potential eliminating agents–acid deposition, climate change, deer, beech sprouts. But before we can convict any of them we need to know that there has been a crime. Have we any evidence that some groundlayer species were commoner in the past than they are now?

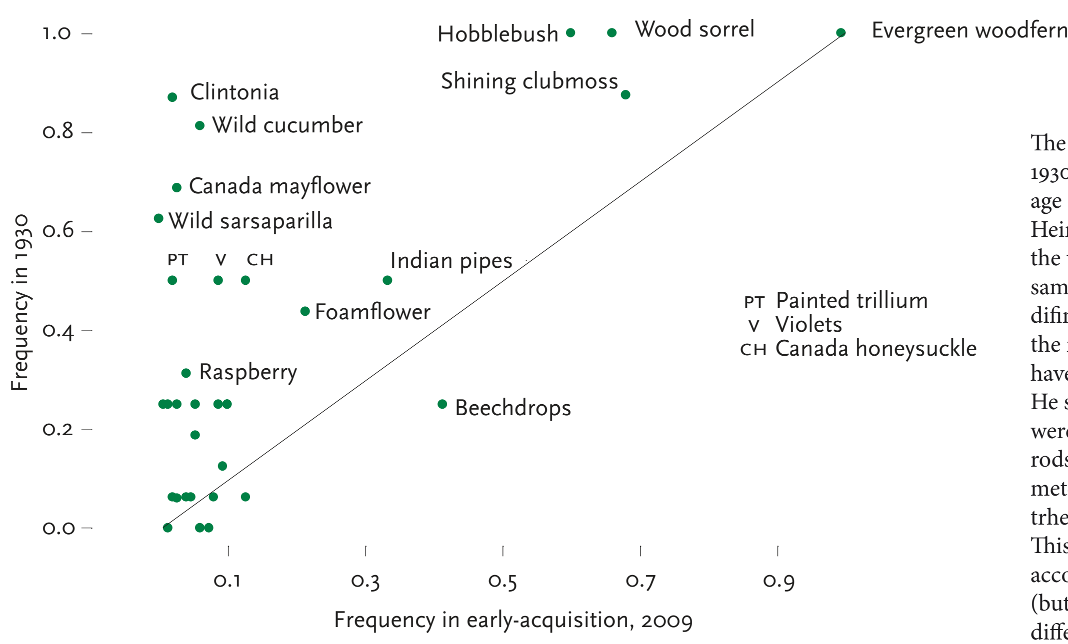
Thus far, we have found only one account of early Adirondack groundlayers. In the early 1930s, Carl Heimburger, a graduate student in the Laboratory of Forest Soils under Charles Pack at Cornell University, sampled about 130 plots scattered throughout the Adirondacks, in a remarkably detailed study of forests types and forest soils. His goal, a phytosociological classification of understory vegetation that would describe "natural" forest types and forest growth, seems old-fashioned to us. But his botany was first rate–he had the assistance of K.A. Weigand, S.H. Burnham, and A.L. Andrews–and his species tables are the most detailed look at historical Adirondack forest floras that we know of.

Much of the land we sampled would have fallen into his viburnum-oxalis (VO) forest type, which he describes as a mixed spruce-hardwoods forest covering "by far the largest area of the Adirondacks" of any of his forest types. He lists 38 species of upland herbs for his 16 samples of VO forests. We found 34 of them in our plots. Two of the remaining ones (trout lily, large-leaved goldenrod) occur in the central Adirondacks; we may just have not been in the right place at the right time to see them. The other two (the rattlesnake orchids *Goodyera repens* and *tessellata*) are quite rare in the central Adirondacks, and may have changed their abundance since 1930.

We think it quite significant that Heimburger's species list for ordinary spruce-hardwoods forests contains none of the species like silvery spleenwort or blue cohoosh that we associate with fertile sites. He describes these species in some detail, but says they are rare and local and associated special geological and topographic situations–very much the places where we find them today.

It is possible, at least for the common species, to make a rough comparison of the frequency at which Heimburger saw the common species to the frequency at which we did. The comparison is only approximate. He had relatively few sample plots, did not place them randomly, and sampled them by tossing a Raunkiaer ring, an method that goes back to the early days of plant ecology.*

FREQUENCIES OF GROUNDLAYER SPECIES, HEIMBERGER (1930-1932) VS. OUR STUDY



The frequency in 1930 is the percentage of sites at which Heimburger say the the species. His sample areas were difined by tosses of the ring and did not have a fixed area. He says that they were about 6 square rods or 151 square meters, about twice trhe size of ours. This, by itself, could account for some (but not all) of the difference between his frequencies and ours.

The graph compares the frequency of some common understory plants in his 16 viburnum-oxalis plots to their frequency in our 180 early-acquisition plots.

The results are interesting. Our work matches his well in the sense that every species that was common in our plots was also common in his. But his work also differs from ours in a significant way: there are 6 species in the upper left-hand of the chart that were five times or more as important in his plots as ours.

Some of the differences may reflect his sampling methods (note on p. 43), and some reflect the loss of frost-sensitive species like clintonia and painted trillium during our survey. But others may well be real change. Trilliums, for example, are both frost sensitive and deer sensitive, and we have fairly good evidence that Adirondack deer populations have changed in the last 80 years.

Possible Changes in Unharvested Forests Summing up, the two historical studies just described suggest that:

> The overall species lists of unharvested Adirondack forests have changed little in the last 80-110 years. In particular, there is no evidence that either the trees or the herbs which we associate with fertile sites were more widespread then than now.
>
> The average sizes of trees in unharvested forests seems to have changed little since 1900.
>
> The average abundances of the dominant trees may have changed. Red spruce, yellow birch, and hemlocks may have declined, and red maple increased.
>
> All the herbs that are common now also seem to have been common in these forests 80 years ago. But several herbs that are frequent but not common now–clintonia, wild cucumber, Canada mayflower, wild sarsaparilla, painted trillium, and violets–may have declined.

SUMMARY

Our results suggest answers to 8 questions.

1 How strongly differentiated are the early-acquisition forests of the central Adirondacks?

Very strongly in the size (and hence likely in the age) of their largest trees, more weakly in their canopy composition, little at all in their subcanopies, understories and ground layers.

Exactly as Barbara McMartin suggested, the early-acquisition forests we examined had more large trees, both living and dead, than no-recent-harvest and harvested forests. They also had more yellow birch, and in some cases more hemlock. But their subcanopies and understories were dominated by beech, exactly as were the subcanopies and understories of the younger forests. Their groundlayers and bryofloras were similar to those of younger forest, but seemed to have more moss cover, and had three bryophytes, *Neckera pennata, Porella platyphylla,* and *Anomodon attenuatus,* that were largely absent from recently harvested forests.

2 Are early-acquisition forests more diverse than younger ones? Do they have specialized forest-interior plants that are more abundant than in younger forests?

No to the first question; they are, if anything, less diverse to the second. And barely to the second. The three bryophytes just mentioned, *Neckera, Anomodon* and *Porella,* clearly meet our criteria (p. 4) for forest interior species. The foam flower may be as well. No others do.

3 How similar are early-acquisition and later acquisition (= no-recent-harvest) forests?

The answer varies with the forest and the property. Some later-acquisition forests probably have had very little harvesting and strongly resemble early-acquisition forests; others are more like harvested forests. Overall, the no-recent-harvest forests that we examined were similar in diversity to early-acquisition forests and like them tended to have many frees over 50 cm in diameter. But they had less basal area, less moss cover, and more beech than early-acquisition forests. In these respects they resembled harvested forests.

4 To what extent do Forest Preserve lands elsewhere in the Adirondacks resemble the ones we studied?

They seem to resemble the ones we studied fairly strongly in their dominant tree species and in the abundance of large trees. But they had more early-succession and fertile-soil trees than our forests, and so their canopies were on average more diverse.

5 How uniform are the ground layers of central Adirondack hardwood forests?

Extremely uniform, as long as you stay on dry or mesic sites and avoid roads and large gaps. Basically it is the same 5-10 species over and again over and everything else casually or rarely. The community changes when you are under conifers or on wet soils, or if you strike one of the rare coves with moist fertile soils. Otherwise it hardly changes at all.

6 What are the effects of harvesting on understory diversity?

In the low-diversity forests we were examining, harvesting increases diversity by introducing disturbance and gap species.

7 Are deer affecting diversity?

We do not know. We know from direct observations that the most intensely browsed areas have low diversity. But we have no idea how frequently this happens or whether deer are reducing the average abundance of particular species. The question is an important one, and we would like to know the answer.

8 How similar were the forests of a century ago to the early-acquisition forests we studied?

From the limited historical information we have found the canopy species are the same and reached similar sizes, but red spruce, hemlock, and yellow birch were more abundant, red spruce dramatically so. The common ground layer species today were common then, but six herbs (clintonia, Canada mayflower, painted trillium, red trillium, bellwort, wild cucumber) that were occasional in our plots may have been more abundant in 1930.

IMPLICATIONS FOR CONSERVATION, MANAGEMENT, AND RESEARCH

The findings of this study add to our knowledge of early-acquisition forests in five ways.

They confirm that many early-acquisition forests contain large trees and snags, and are structurally different from later-acquisition forests. Moreover, the ease with which we found large trees in every early-acquisition forest we visited suggests that, as Barbara McMartin conjectured in 1994, the total area with such trees in the Adirondacks is several hundred thousand acres or more.

They also confirm that the majority of central Adirondack forests, irregardless of their cutting history, have patchy canopies and dense understories of young beech. Mixed-species forests with tall continuous canopies still exist but are rare.

They show, for the first time, that almost all central Adirondack forests are low in ground-layer diversity and have almost no forest-interior plant species.

They also show, as many workers have suspected, that ground-layer diversity is largely independent of forest history and that early-acquisition forests have, if anything, fewer groundlayer species than harvested ones.

And finally they suggest a surprising amount of cryptic historical change: early-acquisition forests without harvesting, fires, or storms seem to have seen significant decreases in 3 of their 6 major canopy species and 6 of their 9 commonest herbs.

Implications for Conservation Conservationists may want to note that:

Both early-acquisition and the no-recent-harvest lands in the Forest Preserve are significant reservoirs of big old trees. The early-acquisition lands, in particular, are unique in the Northeast. Every stand we entered had some giant trees, and in many stands they went on for miles and miles.

Stands with big trees also occur on private lands, but they are small and uncommon and the trees are never as big. Protecting the stands on private lands may be of local importance. But from a regional perspective, most of the big trees are on public lands, and so most of them are already protected.

This protection guarantees that the big trees will not be cut, but it doesn't guarantee that they will be replaced by other big trees when they die. The early-acquisition forests may be more dynamic that we thought. The apparent loss of spruce and yellow birch from the canopies of unharvested forests in the last century suggests that other species could be lost in this one. The abundance of young beech sprouts in forest understories suggests that it will be increasingly hard for other canopy species to replace themselves as old trees die.

The early-acquisition forests are protecting big trees but not groundlayer diversity. With a few local exceptions, their groundlayer diversity are species poor. High diversity stands occur, especially in the Champlain and Hudson watersheds, but they are small and rare. We do not, at present, know where they are, or how to predict their occurrence, or how many of them are currently protected.

Implications for Forest Management Forest managers may want to note that:

Stands with large trees are quite rare on private lands. Strong arguments can be made for preserving them for their own sake, and because they may be important for birds, amphibians, invertebrates, and a few forest-interior bryophytes. But there is no evidence that they are important for vascular plant diversity.

Similar arguments apply to using management or reserves to create stands with late-successional structure. There are good reasons to do this for its own sake and for animals and for bryophytes. But there is no evidence that it will improve vascular plant diversity, and some evidence that it may decrease it.

Protecting big trees is relatively easy. Maintaining them in a forest may be hard or impossible. The cumulative effects of acid deposition, climate change, and the dominance of beech in forest understories may be hard to overcome. It is quite possible that few stands with big trees, whether original or newly created, will survive more for another forest generation.

Stands with high groundlayer plant diversity, usually associated with species that require fertile soils, are rare everywhere in the Adirondacks. There are strong arguments for preserving them for their rarity values, and also for their beauty: they are by far our best wildflower stands.

Implications for Research Researchers may want to note that:

Undisturbed forests may be more dynamic than we thought. Their composition, and hence their carbon storage, can change in unexpected ways. We need to be watching them and trying to explain the changes. This study may serve as a useful baseline.

Understory diversity in Adirondack forests is very unequally distributed. It is low almost everywhere and high in a few spots. We do not as yet know what makes these hotspots, how many of them there are, how they are distributed, or whether they are protected. We ought to.

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