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RICH MESIC FORESTS: EDAPHIC AND PHYSIOGRAPHIC
DRIVERS OF COMMUNITY VARIATION IN
WESTERN MASSACHUSETTS

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ABSTRACT. Rich Mesic Forest, a Northeastern variant of the species-rich Mixed Mesophytic Forest association of eastern North America, is an *Acer saccharum*-dominated forest type typically associated with calcareous bedrock and nutrient-rich, mull soils. Rich Mesic Forest (RMF) is a priority for conservation in the Northeast due to its limited areal extent, high plant species richness, and numerous rare taxa, yet the community characteristics and environmental correlates of this forest type are incompletely understood. This study undertook a quantitative classification of RMF of the northeastern edge of the Berkshire Plateau in western Massachusetts. Cluster analysis of data from ten sites identified two vegetation types within the RMF community, the *Acer saccharum*–*Allium tricoccum*–*Caulophyllum thalictroides* Type (AAC) and the *Acer saccharum*–*Dicentra cucullaria*–*Polystichum acrostichoides* Type (ADP); in addition, two subtypes were distinguished within ADP. Ordination of vegetation data using detrended correspondence analysis identified increased soil pH and calcium concentration as key environmental factors associated with variation within RMF and differentiation of RMF from the typical northern and transition hardwoods vegetation of the region. On sites with high soil pH and nutrients, vegetation variation was primarily associated with physiography, particularly the presence of exposed bedrock and solar insolation levels as controlled by slope and aspect. Occurrences of RMF on steep sites with frequent bedrock exposures and high insolation provide habitat for uncommon plant species reaching their northeastern range limits in the Northeast, and are of particular interest for biodiversity conservation. Comparisons between the results of this study in western Massachusetts and prior research on Mesophytic Forests in other regions of eastern North America illustrate a striking constancy in species composition, with over 70% of common species in Mesophytic Forests of the Southeast and Midwest also being recorded in RMF in our study region.

Key Words: Rich Mesic Forest, Mixed Mesophytic Forest, forest herbs, western Massachusetts, species richness, conservation

Rich Mesic Forest (RMF) is a northeastern variant of the species-rich Mixed Mesophytic Forest association of the southern Appalachian Plateaus of eastern North America (Braun 1950). Plant species associated with Mixed Mesophytic Forest (hereafter “Mesophytic Forest”) compose a significant percentage of total plant diversity in

the eastern deciduous forest biome (Braun 1950), including numerous rare species in the Northeast (Swain and Kearsley 2000; Thompson and Sorenson 2000). Mesophytic Forest and its northern variants have been recognized as priorities for conservation throughout their range (e.g., Duffy and Meier 1992; MacDougal 2001; Swain and Kearsley 2000). While numerous studies have investigated Mesophytic Forests in the Southeast and Midwest (e.g., Braun 1950; Curtis 1959; Daubenmire 1936; Graves and Monk 1982), few studies have quantitatively evaluated examples of this community type in the Northeast. The objectives of this study were: (1) to describe RMF vegetation composition, structure, and variation in western Massachusetts where the community is well represented; (2) to relate observed vegetation patterns to environmental gradients; and (3) to compare Northeastern RMF with Mesophytic Forests throughout eastern North America.

Rich Mesic Forest is distinguished from northern and transition hardwoods vegetation by numerous taxa not commonly found in other forest types in the Northeast, including many ferns and spring-flowering herbs. The canopy of RMF is typically dominated by *Acer saccharum*, with lesser amounts of *Fraxinus americana*, *Carya cordiformis*, and *Tilia americana* (Weatherbee 1996). Shrub and sapling layers tend to be sparse and often consist of tree species found in the canopy and *Ostrya virginiana* (Weatherbee 1996). In addition to *A. saccharum* dominance, RMF is distinguished by the composition and structure of the herbaceous layer: both species richness and herb layer cover tend to be high relative to other forest types (J. Jenkins, White Creek Field School, White Creek, NY, unpubl. data; Swain and Kearsley 2000; Thompson and Sorenson 2000). Characteristic RMF herbaceous species include spring ephemerals such as *Allium tricoccum* and *Dicentra cucullaria*, spring-flowering herbs such as *Asarum canadense*, *Caulophyllum thalictroides*, and *Sanguinaria canadensis*, and ferns such as *Adiantum pedatum* and *Dryopteris goldiana* (Swain and Kearsley 2000; Weatherbee 1996).

Previous reports on RMF in the Northeast have been primarily qualitative descriptions in regional vegetation classifications and floras (e.g., Swain and Kearsley 2000; Weatherbee 1996; Weatherbee and Crow 1992). Forest types similar to RMF have also been referred to as “rich northern hardwood forest” (Thompson and Sorenson 2000), “beech-maple mesic forest” or “maple-basswood rich mesic forest” (Reschke 1990), “rich sugar maple forests” (Nault and Gagnon 1988), and a northern variant of southeastern Mesophytic Forest (Gauch and Stone 1979; Parnall 1998). Forest vegetation, including many plant

species typical of RMF in southern New England, has been documented as far north as the northern edge of the deciduous forest zone in Quebec and New Brunswick (MacDougal 2001; Nault and Gagnon 1993).

In general, RMF vegetation is best developed in western New England and adjacent New York. However, even within this area RMF sites tend to be limited in extent and closely associated with unique physiographic and geologic settings: primarily mesic easterly slopes over bedrock with calcareous influence (Parnall 1998; Thompson and Sorenson 2000; Weatherbee 1996). Further, RMF sites are often associated with mull soil, a forest soil type consisting of a mixture of well-humified organic matter and mineral soil, often with crumb or granular structure, a gradual transition between the A and B soil horizons, and absence of a well-developed O layer (Gregorich et al. 2002). In addition to these environmental correlates, our prior analyses of RMF vegetation variation in relation to 19th century agricultural land-use patterns in two towns in Franklin County, Massachusetts indicate that past human disturbance is an important determinant of modern RMF distribution and species composition (Bellemare et al. 2002). The present study focuses on well-developed examples of RMF vegetation across a larger geographic area, incorporating various bedrock and soil types and a broader array of physiographic settings in an effort to identify key environmental gradients that influence variation in RMF vegetation.

MATERIALS AND METHODS

Description of study area. The study area was a 50 by 30 km region in western Franklin and Hampshire Counties in western Massachusetts (Figure 1). Regional forest types include Transition Hardwoods–White Pine–Hemlock and Northern Hardwoods–Hemlock–White Pine (Westveld 1956), although forest stands sampled for this study were primarily *Acer saccharum*-dominated with few conifers. The study area lies in the northeastern foothills of the Berkshire Plateau, a region of predominantly metamorphosed schists of Paleozoic origin, principally the Gile Mountain, Waits River, Goshen, Hawley, and Moretown formations (proceeding roughly east to west across study area, respectively). The Gile Mountain and Waits River formations are composed primarily of quartz-mica schists with interbeds of calcareous granofels and quartzose marble (Zen 1983); marble interbeds up to ~ 9 m thick are present in some areas of the Waits River formation (Segerstrom 1956). The Goshen formation is composed primarily of micaceous quartzite or quartz schist grading to carbonaceous aluminous

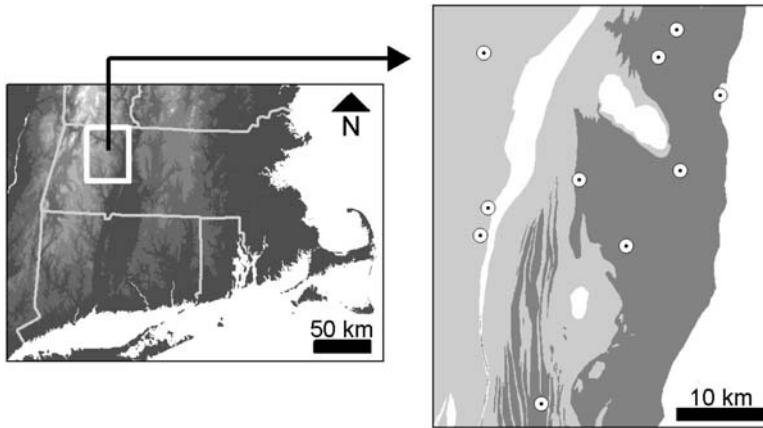


Figure 1. Topography of southern New England and the location of the study area on the eastern edge of the Berkshire Plateau in western Massachusetts (left). Elevations range from near sea level (dark gray) to 1100 m (light gray). Study sites (circles) and simplified bedrock geology (shading) are indicated on the enlarged inset (right). Dark gray areas are characterized by schists with frequent calcareous influence (beds of calcareous granofels or quartzose marble; includes Waits River, Gile Mountain, and Goshen formations, in part); light gray areas are predominantly schists, phyllites, and granofels with occasional calcareous influence (includes Moretown, Hoosac, and Goshen formations, in part); white areas include gneisses and schists that are typically lacking in calcareous influence (includes Shelburne Falls and Goshen Domes and Hawley formation, in part). Modified from MassGIS (2004) and Zen (1983).

schist; interbeds of calc-silicate or calcareous granofels up to ~ 2 m thick occur in parts of this formation (Hatch et al. 1970; Zen 1983). The Hawley and Moretown formations are composed of schists, granulite, and amphibolite, with marble interbeds typically absent (Chidester et al. 1967). Physiographically, the study area is a dissected upland covered mainly by loamy soils developed in glacial till derived from schist bedrock (Anonymous 1995; Segerstrom 1956); upland soils in the area tend to be “very strongly” to “moderately” acidic (Anonymous 1995; Mott and Fuller 1967). Study sites ranged in elevation from ~ 150 to 500 m above sea level. The climate is continental, with a January mean temperature of -5.1°C and a July mean temperature of 21.1°C ; precipitation is evenly distributed throughout the year, with an average annual total of 119 cm (Mott and Fuller 1967).

Data collection. Herbaceous indicator species for RMF (Table 1) were identified from literature (e.g., Weatherbee 1996) and field

Table 1. Herbaceous indicator species of Rich Mesic Forests in western Massachusetts, adapted from Weatherbee (1996) and field observations of the lead author.

Taxa	Common Names
<i>Actaea alba</i>	Doll's eyes
<i>Actaea rubra</i>	Red baneberry
<i>Adiantum pedatum</i>	Maidenhair fern
<i>Allium tricoccum</i>	Wild leek
<i>Asarum canadense</i>	Wild ginger
<i>Athyrium pycnocarpon</i>	Glade fern
<i>Cardamine concatenata</i>	Five-parted toothwort
<i>Cardamine diphylla</i>	Broad-leaved toothwort
<i>Cardamine</i> × <i>maxima</i>	Three-leaved toothwort
<i>Carex plantaginea</i>	Plantain-leaved sedge
<i>Caulophyllum thalictroides</i>	Blue cohosh
<i>Dicentra canadensis</i>	Squirrel corn
<i>Dicentra cucullaria</i>	Dutchman's breeches
<i>Dryopteris goldiana</i>	Goldie's fern
<i>Hepatica acutiloba</i>	Sharp-lobed hepatica
<i>Hydrophyllum virginianum</i>	Eastern waterleaf
<i>Osmorhiza claytonii</i>	Bland sweet cicely
<i>Sanguinaria canadensis</i>	Bloodroot
<i>Thalictrum dioicum</i>	Early meadow rue

observations of the lead author; these species tend to be common at RMF sites and are largely absent from other forest vegetation types in the region (Smith 1995). Field reconnaissance of the study area in the spring and summer of 1999 identified over twenty-five forest sites of varying extent and species composition where populations of RMF indicator species occurred. Of these, ten study sites were selected that were representative of the range of RMF vegetation in the study area, including sites with high frequency and cover of RMF indicator species, as well as sites with low frequency and cover of RMF indicator species. Between November 1999 and March 2000, thirty-six 20 × 20 m plots were established, with three to six plots randomly located at each site depending upon site areal extent and heterogeneity. Plots were subdivided into four 10 × 10 m subplots in which vegetation and environmental measurements were made and subsequently averaged for the whole plot.

Live and dead trees ≥ 2.5 cm diameter at breast height were tallied for species, canopy position, and diameter at breast height (DBH) between November 1999 and March 2000. Herb layer vegetation was sampled at all sites between May 1 and May 26, 2000; this sampling

period was selected so as to capture spring ephemeral herbs which senesce early in the summer, while still allowing for identification of emergent summer-green herbs. Herb-layer species percent cover, including tree seedlings and shrubs, were assessed for all vascular plant taxa ≤ 1 m in height using modified Braun-Blanquet cover classes: 0–1%, 1–12%, 12–50%, 50–75%, and 75%+. Nomenclature follows Gleason and Cronquist (1991); taxa tentatively identified to species are indicated with a cf. (= *circa forma*) designation. Taxa that were grouped for analysis due to difficulty in distinguishing between non-reproductive individuals included *Actaea alba* and *A. rubra*, *Aster lanceolatus* and *A. lateriflorus*, *Dicentra canadensis* and *D. cucullaria*, *Galium circaezans* and *G. lanceolatum*, *Impatiens capensis* and *I. pallida*, *Prenanthes* species, and *Vitis* species. Records of several *Carex* species were also combined due to the difficulty of reliably distinguishing between certain groups of taxa, with *C. leptonevia*, *C. blanda*, and *C. laxiflora* combined as *C. laxiflora s.l.*, records of *C. rosea* and *C. radiata* combined as *C. rosea s.l.*, and records of *C. swanii* and *C. virescens* combined as *C. swanii s.l.* Records of the grass species *Glyceria striata* and *G. melicaria* were also combined for analysis, and 2 records each of *Poa* spp. and *Agrostis* spp. were not identified to species.

Cover of exposed bedrock, rocks, and coarse woody debris (CWD) was estimated and aspect and slope were recorded in each subplot. To assess microtopography, a qualitative estimate of the degree of pit and mound topography was noted within each subplot. Soil moisture levels were assessed in three ways: first, terrain shape index (TSI) values were calculated to estimate the relative concavity or convexity of each subplot by measuring slope in eight directions from the center of each subplot (N, NE, E, SE, S, SW, W, and NW; McNab 1989); second, a qualitative measure of soil moisture class (1 = somewhat moist, 2 = moist, 3 = very moist) was estimated in each subplot; third, the presence of seeps or small ephemeral streams in subplots was recorded. Distance up to 50 meters to the nearest bedrock outcrop was estimated to within 5 meters. Solar insolation for each plot during the month of May was calculated using a model incorporating aspect, slope, elevation, latitude, and longitude (Ollinger et al. 1995). These estimates of insolation level differentiate plots based primarily on local physiography (i.e., slope and aspect); they do not incorporate canopy attenuation of light, which becomes a critical factor influencing light levels in the forest understory following canopy leaf-out in late spring (Neufeld and Young 2003). In regards to the herbaceous layer, these estimates of insolation may be considered as a general index of light levels and temperature prior to

canopy leaf-out, when a substantial percentage of incident light reaches the forest floor (Neufeld and Young 2003). Following canopy leaf-out, variation in insolation levels may continue to influence temperature and water status in the understory (Cantlon 1953), but the relationship between insolation and light levels in the herbaceous layer is likely confounded by canopy attenuation.

Mineral soil samples (0–15 cm) were collected from the center of each subplot using a 15 cm PVC (polyvinyl chloride) cylindrical corer with an inside diameter of 5.1 cm. Samples were air-dried, and then oven dried at 105°C for 48 hours. Bulk density was calculated after samples were sieved to 2 mm (Federer et al. 1993). Subsamples of each soil core were analyzed by Brookside Laboratories, New Knoxville, OH to determine total exchange capacity (TEC) and exchangeable cation concentrations (Mehlich 1984), pH (McLean 1982), percent organic matter (SOM%; Store 1984), and particle size distribution (Anonymous 1998). Total soil carbon and nitrogen content were measured by dry combustion using a Fisons C:N analyzer (Fisons Instruments, Beverly, MA) at Harvard Forest after subsamples were pulverized with mortar and pestle and oven-dried for 12 hours at 70°C.

Data analysis. Herb layer species abundance data were classified in PCORD (version 4, MjM Software Design, Gleneden Beach, OR) using the Sorensen (Bray-Curtis) metric and agglomerative cluster analysis (flexible $\beta = -0.25$; Greig-Smith 1983) to identify vegetation types and subtypes. Detrended correspondence analysis (DCA; Hill 1979) in PCORD was used to ordinate herb layer data and to identify environmental gradients corresponding with the primary axes of vegetation variation. Other ordination techniques, such as nonmetric multidimensional scaling (NMS), produced qualitatively similar results to DCA (results not presented).

Nonparametric Mann-Whitney tests in the Kruskal-Wallis test procedure of SYSTAT (version 9, SPSS, Inc., Chicago, IL) were used to evaluate differences in environmental variables, canopy and subcanopy tree basal area, and species richness among the vegetation types and subtypes identified by cluster analysis. Differences in herb layer species abundance (i.e., % cover) among vegetation types and subtypes were analyzed with Mann-Whitney tests for taxa occurring in two or more plots of each group compared. Fisher's Exact tests in SYSTAT were used to evaluate differences in individual species frequency among vegetation types and subtypes for taxa with ≥ 3 presences and $\leq 90\%$ overall frequency in the groups compared. The

Table 2. Canopy and subcanopy composition of RMF vegetation types, based on frequency of occurrence (F %) and basal area (BA). Only species occurring in two or more plots/strata are included. Differences in basal area among ADP and ACC types were analyzed with Mann-Whitney tests; significance levels: * = $p \leq 0.05$, ** = $p \leq 0.01$. Sample sizes: ADP, n = 26; AAC, n = 10.

	ADP		AAC	
	F %	BA (m ² /ha)	F %	BA (m ² /ha)
Canopy				
<i>Acer saccharum</i>	96	14.43	100	12.65
<i>Fraxinus americana</i>	69	5.79	60	3.62
<i>Fagus grandifolia</i>	38	1.18*	0	0.00
<i>Quercus rubra</i>	8	0.87	30	2.64
<i>Carya cordiformis</i>	27	0.72	50	2.28
<i>Tilia americana</i>	23	0.57	30	0.40
<i>Betula lenta</i>	23	0.57	10	0.02
<i>Tsuga canadensis</i>	12	0.54	0	0.00
<i>Betula alleghaniensis</i>	23	0.42	0	0.00
<i>Ostrya virginiana</i>	19	0.36	10	0.09
<i>Betula papyrifera</i>	12	0.25	0	0.00
<i>Prunus serotina</i>	19	0.24	0	0.00
<i>Ulmus rubra</i>	4	0.12	10	0.28
<i>Ulmus americana</i>	4	0.00	20	1.50
Subcanopy and Saplings > 2.5 cm DBH				
<i>Acer saccharum</i>	100	1.35	100	1.72
<i>Fagus grandifolia</i>	85	0.57**	10	0.01
<i>Ostrya virginiana</i>	85	0.17	90	0.44
<i>Betula alleghaniensis</i>	54	0.13*	10	0.03
<i>Acer pensylvanicum</i>	50	0.12**	0	0.00
<i>Tsuga canadensis</i>	15	0.09	0	0.00
<i>Fraxinus americana</i>	27	0.09	20	0.03
<i>Betula lenta</i>	27	0.08	20	0.03
<i>Tilia americana</i>	38	0.07	40	0.08
<i>Carya cordiformis</i>	8	0.04	20	0.05
<i>Ulmus rubra</i>	19	0.02	10	0.00
<i>Acer spicatum</i>	8	0.02	0	0.00
<i>Carpinus caroliniana</i>	4	0.01	30	0.03*
<i>Ulmus americana</i>	4	0.01	10	0.01
MEAN TOTAL basal area	–	30.67	–	28.37

results of numerous individual Mann-Whitney and Fisher's Exact test analyses are presented in Tables 2–6 and Bonferroni corrections (Rice 1989) for table-wide or overall error rate have not been included; consequently, some significant results may be spurious and marginally significant results should be interpreted with caution.

Table 3. Herb layer species frequency (F %) for all RMF plots, and species frequency (f %) and mean cover (c %) for the ADP and AAC vegetation types. Taxa are arranged by relative strength of association with vegetation types, those at the top of the table being strongly associated with ADP and those at the bottom being strongly associated with AAC. Only taxa with $\geq 25\%$ frequency overall or exhibiting significant association ($p \leq 0.05$) with one type are listed. Congeners that were not distinguished are indicated by genus and “spp.”; taxa only tentatively identified to species are indicated with a cf. (= *circa forma*) designation. *Carex leptonevia* (Fernald) Fernald, *C. blanda* Dewey, and *C. laxiflora* Lam. were combined as *C. laxiflora s.l.* (= *sensu lato*). Differences in species frequency and abundance between ADP and AAC types were tested with Fisher’s Exact and Mann-Whitney tests, respectively. NT = no test conducted. Sample sizes: RMF, n = 36; ADP, n = 26; AAC, n = 10.

	RMF	ADP	AAC	Mann-Whitney <i>p</i>			
Community Level							
Species richness (median)	49	49	48	0.901			
Total herb layer cover % (median)	23	22	32	0.006			
Species Level							
Taxa	RMF	ADP		AAC		Fisher’s <i>p</i>	Mann-Whitney <i>p</i>
	F %	f %	c %	f %	c %		
<i>Acer pensylvanicum</i>	53	73	1.06	0	0.00	< 0.001	NT
<i>Viola blanda</i>	47	65	0.23	0	0.00	< 0.001	NT
<i>Uvularia sessilifolia</i>	39	54	0.33	0	0.00	0.003	NT
<i>Botrychium virginianum</i>	31	42	0.11	0	0.00	0.016	NT
<i>Dryopteris intermedia</i>	69	88	2.03	20	0.03	< 0.001	< 0.001
<i>Osmorhiza claytonii</i>	61	77	0.56	20	0.04	0.005	0.001
<i>Viola rotundifolia</i>	31	42	0.17	0	0.00	0.016	NT
<i>Dennstaedtia punctilobula</i>	28	38	0.15	0	0.00	0.035	NT
<i>Dicentra</i> spp.	75	88	4.59	40	0.15	0.006	0.001
<i>Fagus grandifolia</i>	50	65	1.01	10	0.01	0.007	NT
<i>Claytonia caroliniana</i>	64	77	0.81	30	0.06	0.018	0.001
<i>Tiarella cordifolia</i>	67	77	1.01	40	0.25	0.053	0.014
<i>Maianthemum canadense</i>	36	46	0.25	10	0.01	0.060	NT
<i>Athyrium thelypteroides</i>	67	77	2.71	40	0.26	0.053	0.048
<i>Cardamine diphylla</i>	50	58	0.45	30	0.06	0.264	0.046
<i>Viburnum acerifolium</i>	28	35	0.24	10	0.01	0.223	NT
<i>Panax quinquefolius</i>	25	31	0.07	10	0.01	0.392	NT
<i>Betula</i> cf. <i>alleghaniensis</i>	44	54	0.12	20	0.03	0.133	0.053
<i>Laportea canadensis</i>	42	50	0.48	20	0.03	0.142	0.058
<i>Quercus rubra</i>	36	42	0.09	20	0.03	0.270	0.171
<i>Prunus serotina</i>	50	58	0.14	30	0.05	0.264	0.097
<i>Mitella diphylla</i>	31	35	0.08	20	0.03	0.688	0.317
<i>Impatiens</i> spp.	44	50	0.58	30	0.09	0.456	0.228
<i>Sambucus racemosa</i>	69	77	0.17	50	0.09	0.224	0.071

Table 3. Continued.

Taxa	RMF		ADP		AAC		Fisher's <i>p</i>	Mann-Whitney <i>p</i>
	F %	f %	c %	f %	c %			
<i>Athyrium filix-femina</i>	53	58	0.57	40	0.06	0.463	0.110	
<i>Viola canadensis</i>	39	42	0.31	30	0.05	0.706	0.304	
<i>Rubus allegheniensis</i>	50	54	0.13	40	0.09	0.711	0.469	
<i>Prenanthes</i> spp.	47	50	0.12	40	0.06	0.717	0.395	
<i>Eupatorium rugosum</i>	64	65	0.33	60	0.61	1.0	0.956	
<i>Carex laxiflora</i> s.l.	42	42	0.22	40	0.24	1.0	0.968	
<i>Carya cordiformis</i>	72	73	0.22	70	0.24	1.0	0.772	
<i>Carex plantaginea</i>	61	62	1.15	60	0.76	1.0	0.523	
<i>Polygonum cilinode</i>	31	31	0.28	30	0.10	1.0	0.897	
<i>Solidago rugosa</i>	31	31	0.05	30	0.08	1.0	0.862	
<i>Aster divaricatus</i>	92	92	0.76	90	1.83	NT	0.525	
<i>Trillium erectum</i>	97	100	0.77	90	0.54	NT	0.880	
<i>Acer saccharum</i>	100	100	1.33	100	2.28	NT	0.172	
<i>Caulophyllum thalictroides</i>	100	100	3.59	100	9.90	NT	0.082	
<i>Arisaema triphyllum</i>	92	88	0.55	100	1.53	NT	0.053	
<i>Polystichum acrostichoides</i>	92	88	3.90	100	2.28	NT	0.630	
<i>Actaea</i> spp.	89	88	0.46	90	0.44	1.0	0.957	
<i>Carex pedunculata</i>	50	50	0.17	50	0.08	1.0	0.567	
<i>Tilia americana</i>	56	54	0.14	60	0.13	1.0	0.911	
<i>Viola pubescens</i>	53	53	0.17	50	0.08	1.0	0.816	
<i>Galium triflorum</i>	75	73	0.40	80	0.28	1.0	0.814	
<i>Polygonatum pubescens</i>	83	81	0.45	90	0.78	0.655	0.957	
<i>Fraxinus americana</i>	81	77	0.52	90	0.50	0.645	0.146	
<i>Adiantum pedatum</i>	78	73	0.78	90	2.45	0.397	0.232	
<i>Erythronium americanum</i>	72	69	1.14	80	0.24	0.689	0.440	
<i>Asarum canadense</i>	64	58	0.45	80	0.36	0.270	0.689	
<i>Ostrya virginiana</i>	64	58	0.13	80	0.20	0.270	0.239	
<i>Cornus alternifolia</i>	53	50	0.12	60	0.15	0.717	0.547	
<i>Cardamine</i> × <i>maxima</i>	25	23	0.79	30	0.10	0.686	0.926	
<i>Acer spicatum</i>	31	27	0.13	40	0.08	0.454	0.543	
<i>Dryopteris goldiana</i>	31	27	0.96	40	0.10	0.454	0.696	
<i>Geum canadense</i>	31	27	0.04	40	0.10	0.454	0.315	
<i>Parthenocissus quinquefolia</i>	31	27	0.06	40	0.13	0.454	0.329	
<i>Circaea lutetiana</i>	67	58	0.18	90	0.26	0.115	0.203	
<i>Geranium robertianum</i>	44	38	0.08	60	0.48	0.285	0.143	
<i>Ribes cynosbati</i>	42	35	0.13	60	0.21	0.260	0.085	
<i>Ulmus rubra</i>	42	35	0.07	60	0.10	0.260	0.264	
<i>Hydrophyllum virginianum</i>	33	27	1.91	50	0.25	0.247	0.365	
<i>Rubus occidentalis</i>	33	27	0.05	50	0.14	0.247	0.099	
<i>Rubus odoratus</i>	47	38	0.10	70	0.53	0.139	0.046	
<i>Smilacina racemosa</i>	89	85	0.73	100	4.21	0.559	0.010	
<i>Dryopteris marginalis</i>	75	65	0.95	100	1.35	0.039	0.085	
<i>Aster</i> cf. <i>lanceolatus</i>	19	12	0.01	40	0.08	0.076	0.048	
<i>Carex communis</i>	50	38	0.09	80	0.19	0.060	0.038	

Table 3. Continued.

Taxa	RMF		ADP		AAC		Fisher's <i>p</i>	Mann-Whitney <i>p</i>
	F %	f %	c %	f %	c %			
<i>Ranunculus abortivus</i>	56	46	0.08	80	0.19	0.133	0.029	
<i>Solidago flexicaulis</i>	53	42	0.21	80	3.51	0.065	0.002	
<i>Solanum dulcamara</i>	17	8	0.01	40	0.09	0.039	0.021	
<i>Carex appalachica</i>	69	58	0.25	100	0.30	0.016	0.006	
<i>Cystopteris fragilis</i>	44	31	0.08	80	0.26	0.011	0.003	
<i>Carex albursina</i>	36	23	0.05	70	0.38	0.018	0.002	
<i>Carex platyphylla</i>	14	4	0.01	40	0.10	0.015	NT	
<i>Hepatica acutiloba</i>	17	4	0.02	50	0.64	0.003	NT	
<i>Acer nigrum</i>	8	0	0.00	30	0.05	0.017	NT	
<i>Asplenium trichomanes</i>	8	0	0.00	30	0.06	0.017	NT	
<i>Cystopteris bulbifera</i>	8	0	0.00	30	0.13	0.017	NT	
<i>Cardamine concatenata</i>	8	0	0.00	30	1.50	0.017	NT	
<i>Elymus hystrix</i>	8	0	0.00	30	0.10	0.017	NT	
<i>Carex hitchcockiana</i>	17	0	0.00	60	0.16	< 0.001	NT	
<i>Taraxacum officinale</i>	17	0	0.00	60	0.10	< 0.001	NT	
<i>Allium tricoccum</i>	64	50	1.45	100	10.63	0.006	< 0.001	
<i>Solidago caesia</i>	53	35	0.22	100	1.58	< 0.001	< 0.001	
<i>Oryzopsis racemosa</i>	33	15	0.02	80	0.46	0.001	< 0.001	
<i>Thalictrum dioicum</i>	25	8	0.09	70	2.19	< 0.001	< 0.001	
<i>Saxifraga virginiana</i>	22	0	0.00	80	0.28	< 0.001	NT	
<i>Sanguinaria canadensis</i>	19	0	0.00	70	2.10	< 0.001	NT	

Literature review. A review of ecological and botanical literature was undertaken to identify trends in species composition in the canopy and herbaceous layer of Mesophytic Forests across eastern North America. Twenty-one studies were selected for inclusion based on the author's description of the vegetation sampled as Mesophytic Forest or a related regional variant, or through presence of one or more RMF indicator species in the forest vegetation sampled (Table 1). The studies were divided into three broad geographic regions: the Southeast (including the southern Appalachians and Mid-Atlantic States), the Midwest, and the Northeast (including adjacent Canada); see Appendix 1 for a full list of the studies included and their locations. Only species presence/absence data were compiled due to substantial variation in methods used to estimate abundance. Several caveats apply: (1) while effort was taken to include as many relevant studies as possible, the literature review was not exhaustive; (2) the spatial scale covered by the included studies varied considerably; and (3) the level of floristic detail varied among studies, with some presenting full floras of a given area and others listing only common or dominant species.

Table 4. Total herb layer species richness and cover, and frequency (f %) and mean cover (c %) of individual taxa in subtypes 1A and 1B of ADP. Differences in species richness, total cover, and cover of individual taxa were tested with Mann-Whitney tests. Differences in species frequency among vegetation subtypes were analyzed with Fisher's Exact tests. NT = no test conducted. Congeners that were not distinguished are grouped and indicated by genus and "spp." Only taxa exhibiting significant associations with the subtypes are listed. Sample sizes: Subtype 1A, n = 15; Subtype 1B, n = 11.

	Subtype 1A		Subtype 1B		Mann-Whitney <i>p</i>	
Community Level						
Species richness (median):	44		64		0.002	
Total herb layer cover % (median):	18		24		0.002	
Taxa	Subtype 1A		Subtype 1B		Fisher's <i>p</i>	Mann-Whitney <i>p</i>
	f %	c %	f %	c %		
Subtype 1A Species						
<i>Acer saccharum</i>	100	1.83	100	0.66	NT	0.040
<i>Viola blanda</i>	87	0.36	36	0.06	0.014	0.004
<i>Viola rotundifolia</i>	60	0.26	18	0.05	0.051	0.039
Subtype 1B Species						
<i>Actaea</i> spp.	80	0.43	100	0.50	0.238	0.031
<i>Adiantum pedatum</i>	53	0.47	100	1.20	0.010	0.009
<i>Allium tricoccum</i>	20	0.06	91	3.35	0.001	< 0.001
<i>Athyrium filix-femina</i>	40	0.10	82	1.22	0.051	0.008
<i>Athyrium thelypteroides</i>	60	0.96	100	5.09	0.024	0.001
<i>Carex plantaginea</i>	33	0.32	100	2.28	0.001	0.001
<i>Carya cordiformis</i>	53	0.16	100	0.30	0.010	0.058
<i>Caulophyllum thalictroides</i>	100	2.04	100	5.69	NT	0.047
<i>Circaea lutetiana</i>	33	0.08	91	0.33	0.005	0.001
<i>Dryopteris goldiana</i>	0	0.00	64	2.26	0.001	NT
<i>Eupatorium rugosum</i>	53	0.10	82	0.64	0.217	0.049
<i>Geranium robertianum</i>	20	0.05	64	0.13	0.043	0.049
<i>Geum canadense</i>	7	0.01	55	0.08	0.021	NT
<i>Hydrophyllum virginianum</i>	13	0.03	45	4.48	0.095	0.039
<i>Impatiens</i> spp.	13	0.06	100	1.28	< 0.001	< 0.001
<i>Laportea canadensis</i>	27	0.08	82	1.03	0.015	0.002
<i>Matteuccia struthiopteris</i>	7	0.13	55	1.69	0.021	NT
<i>Mitella diphylla</i>	13	0.02	64	0.16	0.014	0.005
<i>Panax trifolius</i>	7	0.03	55	0.09	0.021	NT
<i>Rubus allegheniensis</i>	33	0.13	82	0.14	0.021	0.295
<i>Rubus idaeus</i>	13	0.02	45	0.42	0.095	0.042
<i>Rubus odoratus</i>	20	0.05	64	0.17	0.043	0.022
<i>Tiarella cordifolia</i>	60	0.53	100	1.68	0.024	0.010
<i>Ulmus rubra</i>	7	0.01	73	0.16	0.001	NT

Table 5. Environmental characteristics of RMF vegetation type sites. Values presented are medians with Mann-Whitney test *p*-values. Sample sizes: ADP, *n* = 26; AAC, *n* = 10.

Environmental Characteristics	ADP	AAC	Mann-Whitney <i>p</i>
Physiographic			
Insolation (MJ/m ² per day)	20.65	22.88	< 0.001
Slope °	20	32	< 0.001
Aspect °	78	110	0.001
Rock % cover	2	10	0.005
Distance to bedrock (m)	7.5	2.5	0.012
Bedrock % cover	1	4	0.024
Coarse woody debris % cover	4	5	0.066
Terrain shape index	0.31	2.69	0.180
Soil Morphology and Texture			
O layer (cm)	1	0	0.001
A horizon (cm)	11	20	0.003
Silt %	30.21	23.71	0.034
Soil organic matter %	8.34	11.45	0.044
Clay %	2.92	3.67	0.049
Bulk density (g/cm ³)	0.59	0.56	0.204
Sand %	66.63	73.13	0.216
Soil moisture class	2	2	0.798
Soil Nutrient Status			
Na ppm	24	38	< 0.001
Cu ppm	1.60	2.67	0.002
C:N ratio	13.22	12.35	0.004
B ppm	0.52	0.67	0.006
Soil Nitrogen %	0.37	0.51	0.008
Soil Carbon %	4.70	6.17	0.013
Fe ppm	232	169	0.023
K ppm	52	66	0.024
Ca ppm	753	1484	0.026
pH	4.7	5.1	0.029
Mg ppm	65	81	0.056
Mn ppm	81	112	0.090
Total exchange capacity	18.65	20.83	0.104
Easily extractable P ppm	36	35	0.633
Soluble Sulfur ppm	36	37	0.659
Al ppm	1110	1107	0.751
Zn ppm	5.16	5.86	0.832

Table 6. Environmental characteristics of Subtypes 1A and 1B of ADP. Values presented are medians with Mann-Whitney test *p*-values. Sample sizes: Subtype 1A, *n* = 15; Subtype 1B, *n* = 11.

Environmental Characteristics	Subtype		Mann-Whitney <i>p</i>
	1A	1B	
Physiographic			
Terrain shape index	-1.33	1.85	0.058
Bedrock % cover	2	0	0.094
Distance to bedrock (m)	7.5	17.5	0.282
Aspect °	80	67	0.299
Insolation (MJ/m ² per day)	20.86	20.32	0.452
Rock % cover	2	2	0.516
Slope °	22	18	0.550
Coarse woody debris % cover	4	4	0.696
Soil Morphology and Texture			
O layer (cm)	1.6	0.3	0.010
A horizon (cm)	7	16	0.029
Clay %	2.92 (+)	2.92	0.039
Sand %	64.75	66.75	0.113
Silt %	30.33	28.83	0.194
Soil organic matter %	7.99	9.58	0.203
Soil moisture class	2	2	0.365
Bulk density (g/cm ³)	0.60	0.58	0.484
Soil Nutrient Status			
Ca ppm	415	1550	0.005
Al ppm	1249	1008	0.005
Mg ppm	42	76	0.006
pH	4.6	4.9	0.016
K ppm	47	65	0.024
B ppm	0.48	0.61	0.029
Zn ppm	4.62	7.27	0.092
Fe ppm	235	229	0.139
Cu ppm	1.31	1.90	0.139
Soluble Sulfur ppm	41	32	0.146
Soil Nitrogen %	0.36	0.39	0.337
C:N ratio	13.25	13.19	0.337
Na ppm	22	29	0.436
Total exchange capacity	17.73	20.75	0.484
Easily extractable P ppm	47	36	0.585
Soil Carbon %	4.47	4.82	0.622
Mn ppm	82	76	0.856

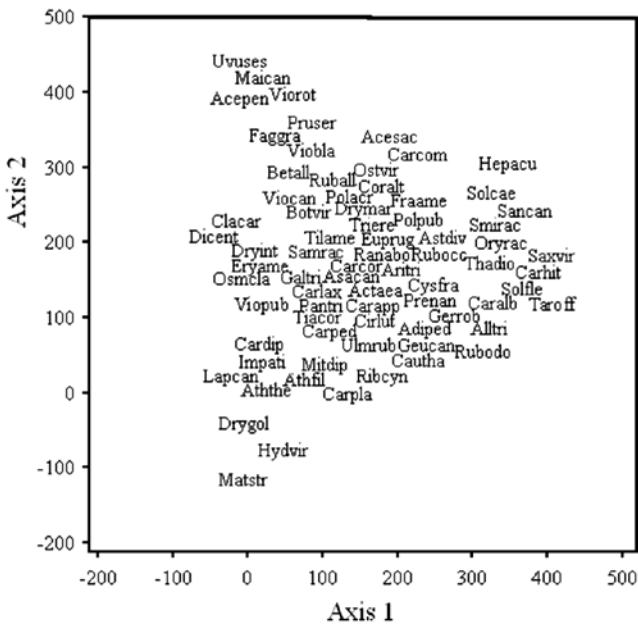
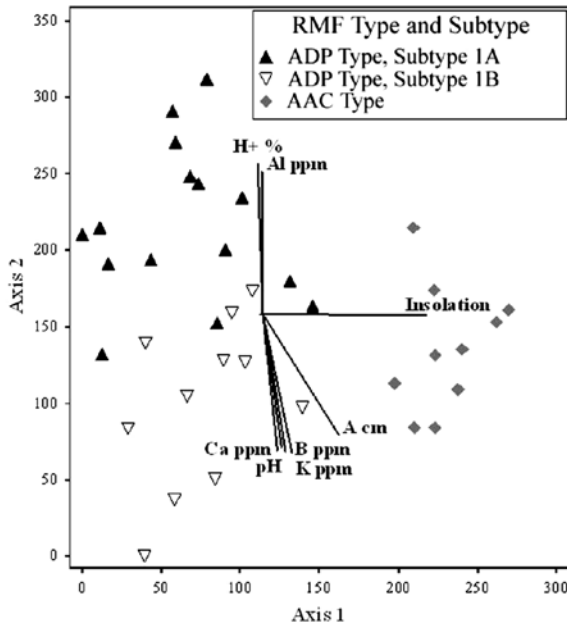
RESULTS

A total of 180 vascular plant taxa were observed in 36 plots, with 175 taxa recorded in the herb layer, 30 woody species recorded in the shrub and sapling layer, and 25 woody species recorded in the subcanopy and canopy (Appendix 2). The mean number of herb layer taxa per plot was 50, with a range from 25 to 74 taxa. The herb layer flora consisted of 110 dicots (62.9%), 40 monocots (22.9%), 24 pteridophytes (13.7%), and 1 gymnosperm ($\sim 0.5\%$). Overall, fifty-eight plant families were represented, with the greatest number of taxa in the Cyperaceae (18 taxa), Asteraceae (15 taxa), and Aspleniaceae (13 taxa).

Vegetation classification. Agglomerative cluster analysis and DCA ordination of vegetation data indicated two distinct vegetation types within RMF (Figure 2). The *Acer saccharum*–*Dicentra cucullaria*–*Polystichum acrostichoides* Type (ADP) incorporated a broad range of RMF vegetation in 26 plots on seven sites. Cluster analysis indicated a further subdivision of two subtypes (1A and 1B) within ADP, corresponding to variation along Axis 2 of the ordination. The *A. saccharum*–*Allium tricoccum*–*Caulophyllum thalictroides* Type (AAC) occurred in 10 plots at the remaining three sites and exhibited less variation. “After-the-fact” coefficients of determination (McCune and Mefford 1999) indicate that the first two axes of the ordination accounted for similar amounts of variance explained (Axis 1 $r^2 = 0.23$; Axis 2 $r^2 = 0.22$).

Acer saccharum was present in all plots and dominated both RMF vegetation types with approximately 50% of the basal area (Table 2). *Fraxinus americana* was the second most abundant canopy tree, comprising 19.1% of the basal area in ADP and 12.9% in AAC. In the subcanopy and sapling layer, *A. saccharum* was present in all plots, along with *Ostrya virginiana* in approximately 90% of plots. Common or abundant herbs in both RMF vegetation types included *Actaea* spp., *Adiantum pedatum*, *Asarum canadense*, and *Caulophyllum thalictroides* (Table 3). Species richness did not differ significantly among the two types; ADP had a median of 49 herb layer taxa per plot (range: 25–74 taxa) and AAC had a median of 48 (range: 39–66 taxa). However, total herb layer cover (%) was significantly higher in AAC than ADP ($p = 0.006$).

***Acer saccharum*–*Allium tricoccum*–*Caulophyllum thalictroides* Type (AAC).** *Fraxinus americana* and *Carya cordiformis* were characteristic associates of *Acer saccharum* in the canopy of AAC. In



the subcanopy, *A. saccharum* and *Ostrya virginiana* were frequent, and *Carpinus caroliniana* exhibited higher basal area than in ADP ($p = 0.035$). Total herb layer cover in AAC was significantly higher than in ADP, (median 32% vs. 22%, $p = 0.006$), resulting in part from the higher abundance of *Allium tricoccum*, *Caulophyllum thalictroides*, and *Smilacina racemosa* in AAC. *Allium tricoccum* was the most abundant herb, with significantly higher mean cover (10.6%) and frequency (100%) than in ADP ($p < 0.01$ for both comparisons). Species such as *Sanguinaria canadensis*, *Saxifraga virginiana*, *Oryzopsis racemosa*, and *Thalictrum dioicum* were significantly more frequent in AAC than in ADP ($p \leq 0.001$ for all 4 taxa). Fern species typical of bedrock exposures, such as *Asplenium trichomanes* and *Cystopteris fragilis*, were also characteristic of AAC vegetation.

***Acer saccharum*–*Dicentra cucullaria*–*Polystichum acrostichoides* Type (ADP).** *Fagus grandifolia* and *Betula alleghaniensis* were characteristic associates of *Acer saccharum* in the canopy of ADP, and were joined in the subcanopy and sapling layers by *A. pensylvanicum* (50% frequency). *Dicentra* spp. were the most abundant herbs (4.6% cover, 88% frequency), and had significantly higher cover and frequency values than in AAC ($p < 0.01$; Table 3). *Dicentra cucullaria* tended to be more common than *D. canadensis* (J. Bellemare, personal observation); however, non-reproductive individuals of the two species were not distinguished and the species were grouped for all analyses. *Polystichum acrostichoides* and *Caulophyllum thalictroides* were also frequent and abundant in ADP; *Trillium erectum* and *Aster divaricatus* were present in over 90% of plots at lower abundance levels. Several herb species were significantly more frequent and abundant in ADP than AAC, including *Claytonia caroliniana*, *Dryopteris intermedia*, and *Osmorhiza claytonii*. Species typical of northern hardwoods vegetation also tended to be more common in the herb layer of ADP, including *A. pensylvanicum* seedlings and *Tiarella cordifolia*.

←

Figure 2. Detrended correspondence analysis ordinations of RMF plots (top) and species (bottom). Vegetation types and subtypes identified by cluster analysis and environmental factors correlated with major axes of variation ($r^2 \geq 0.50$) are indicated. Only taxa occurring in $\geq 50\%$ of plots in one or more of the types or subtypes are labeled. Taxon abbreviations are the first three letters of the genus and specific epithet. Taxa identified to genus only are indicated by the first six letters of the genus name. Included taxa are listed in Appendix 3.

Variation within the *Acer saccharum*–*Dicentra Cucullaria*–*Polystichum acrostichoides* Type. The forest canopy and subcanopy varied little between Subtype 1A and 1B of ADP (data not presented); rather, the subtypes were primarily differentiated by significantly higher species richness and cover in the herb layer of Subtype 1B ($p = 0.002$ for both comparisons; Table 4).

Subtype 1A vegetation was characterized by *Dicentra* spp., *Polystichum acrostichoides*, and *Caulophyllum thalictroides*, each with cover values of 2–5% and frequencies of 80–100%. *Dryopteris intermedia* and seedlings of *Acer pensylvanicum* and *A. saccharum* were also common, the cover of the later being significantly higher in Subtype 1A. *Viola blanda* and *V. rotundifolia* were the only herbaceous species significantly associated with Subtype 1A.

Subtype 1B vegetation was characterized by abundant *Caulophyllum thalictroides*, *Adiantum pedatum*, *Impatiens* spp., *Carex plantaginea*, and *Athyrium thelypteroides* (each with 100% frequency). Numerous herbaceous species exhibited significantly higher frequency and abundance in Subtype 1B, including *Allium tricoccum*, *C. plantaginea*, *Impatiens* spp., and *Laportea canadensis* (Table 4). Likewise, the ferns *Dryopteris goldiana* and *Matteuccia struthiopteris* were common in Subtype 1B, but infrequent or absent from Subtype 1A vegetation.

Environmental variation associated with vegetation patterns. The RMF types ADP and AAC were primarily differentiated along Axis 1 of the ordination (Figure 2). The AAC vegetation type was characterized by high Axis 1 scores, which were positively correlated with solar insolation ($r = 0.77$), soil Na concentration ($r = 0.69$), and slope ($r = 0.66$). Environmental variables negatively correlated with Axis 1 included soil O layer presence and depth ($r = -0.55$), and degree of pit and mound microtopography ($r = -0.44$), the latter likely relating to plot slope, as substantial pit and mound microtopography is unlikely to develop on steep slopes. Plots from ADP and AAC overlapped on Axis 2 of the ordination, although AAC had no plots with high or low Axis 2 scores. Axis 2 scores were positively correlated with soil H^+ % of total ions ($r = 0.75$) and Al concentration ($r = 0.73$). Axis 2 scores were negatively correlated with indicators of soil nutrient status, including Ca concentration ($r = -0.71$) and soil pH ($r = -0.71$), as well as soil A horizon depth ($r = -0.67$) and soil moisture class (i.e., sites with moister soils having lower Axis 2 scores; $r = -0.46$).

The ADP and AAC types differed strongly with respect to physiography and some edaphic variables (Table 5). The AAC plots

had significantly steeper slopes and more southerly aspects, resulting in significantly higher levels of solar insolation than ADP sites ($p < 0.001$). Plots in AAC were also closer to bedrock outcrops, and had higher bedrock and rock cover than ADP plots. The A horizon was significantly deeper in AAC, whereas O layers were more frequent and thicker in ADP. The ADP plots had significantly higher soil silt content, although clay content was significantly higher in AAC. Soil pH and concentrations of Ca, K, and organic matter (SOM) were significantly higher in AAC, as were percent N and C. Soil C:N ratio was significantly lower in AAC.

Subtypes 1A and 1B of ADP vegetation were differentiated along Axis 2 of the ordination, which was associated with a soil pH/nutrient and moisture gradient (Table 6; Figure 2). Soil Ca, Mg, and K concentrations were significantly higher in Subtype 1B than in 1A, as was soil pH. The soil A horizon of Subtype 1B plots was significantly deeper than that of Subtype 1A, whereas O layers were more frequent and thicker in Subtype 1A. Subtypes 1A and 1B did not differ substantially physiologically.

Mixed Mesophytic Forests in eastern North America. Of the 21 studies of Mesophytic Forest vegetation included in the literature review, 18 described canopy species composition. *Acer saccharum* was the most frequently cited tree species (83%), followed by *Fraxinus americana* (61%), *Tilia americana* (61%), and *Fagus grandifolia* (56%; Table 7). In the Southeast, Mesophytic Forest is characterized by a species-rich, “mixed” canopy, including *Liriodendron tulipifera*, *Aesculus flava* Aiton, *Acer saccharum*, *F. americana*, *Fagus grandifolia*, *Carya cordiformis*, and various other species (Braun 1950). In the Northeast, canopy composition is characterized by the increasing dominance of *A. saccharum*, with fewer associates (Tables 2 and 7; MacDougal 2001; Nault and Gagnon 1993). Similarly, Mesophytic Forests in the Midwest are characterized primarily by *A. saccharum* with *T. americana* and *Ulmus* spp. (Curtis 1959; Daubenmire 1936).

Over 300 herb and fern taxa were noted in the 21 studies reviewed. The most commonly cited species were *Caulophyllum thalictroides* (86%) and *Sanguinaria canadensis* (71%), followed by *Allium tricoccum*, *Arisaema triphyllum*, *Hydrophyllum virginianum*, and *Osmorhiza claytonii* (57% each; Table 7). Of the 11 species cited in more than 50% of the studies, all occur frequently in RMF of our study area. In a comparison of species lists for sites in the Northeast and Southeast, 137 herbaceous taxa were noted in two or more studies

Table 7. Common Mesophytic Forest species in eastern North America. Only species cited in > 35% of studies are included, thereby excluding some species that may be characteristic of a particular region, but infrequent or absent in others. Values presented are frequency of citations in all studies and by region (see Appendix 1). P/A = presence/absence in this study.

Species	P/A	All	Northeast	Midwest	Southeast
Tree Species		(n = 18)	(n = 7)	(n = 6)	(n = 5)
<i>Acer saccharum</i>	P	83	100	83	60
<i>Fraxinus americana</i>	P	61	71	33	80
<i>Tilia americana</i>	P	61	57	100	20
<i>Fagus grandifolia</i>	P	56	57	33	80
<i>Carya cordiformis</i>	P	44	29	50	60
<i>Tsuga canadensis</i>	P	39	43	17	60
<i>Liriodendron tulipifera</i> L.	A	39	14	17	100
Herb and Fern Species		(n = 21)	(n = 7)	(n = 6)	(n = 8)
<i>Caulophyllum thalictroides</i>	P	86	100	50	100
<i>Sanguinaria canadensis</i>	P	71	86	100	38
<i>Allium tricoccum</i>	P	57	71	50	50
<i>Osmorhiza claytonii</i>	P	57	71	67	38
<i>Arisaema triphyllum</i>	P	57	57	67	50
<i>Hydrophyllum virginianum</i>	P	57	57	83	38
<i>Dicentra cucullaria</i>	P	52	86	17	50
<i>Erythronium americanum</i>	P	52	86	33	38
<i>Asarum canadense</i>	P	52	71	50	38
<i>Botrychium virginianum</i>	P	52	71	67	25
<i>Smilacina racemosa</i>	P	52	43	100	25
<i>Trillium erectum</i>	P	48	86	17	38
<i>Dicentra canadensis</i>	P	48	57	33	50
<i>Hepatica acutiloba</i>	P	48	57	67	25
<i>Adiantum pedatum</i>	P	43	57	50	25
<i>Carex plantaginea</i>	P	43	57	17	50
<i>Viola canadensis</i>	P	43	57	33	38
<i>Tiarella cordifolia</i>	P	43	43	17	63
<i>Trillium grandiflorum</i> (Michx.) Salisb.	A	43	43	50	38
<i>Geranium maculatum</i>	A	43	29	83	25
<i>Uvularia grandiflora</i> J.E. Smith	A	43	29	67	38
<i>Athyrium pycnocarpon</i>	P	38	43	17	50
<i>Impatiens</i> spp.	P	38	43	33	38
<i>Mitella diphylla</i>	P	38	43	67	13
<i>Thalictrum dioicum</i>	P	38	43	67	13
<i>Galium triflorum</i>	P	38	29	50	38
<i>Laportea canadensis</i>	P	38	29	50	38
<i>Podophyllum peltatum</i> L.	A	38	29	50	38
<i>Claytonia virginica</i> L.	A	38	14	50	50

overall, and of these taxa 74% were cited in both regions. However, many herbaceous taxa typical of southeastern Mesophytic Forests, such as *Cimicifuga racemosa* (L.) Nutt. (cited in 50% of southeastern studies), *Disporum maculatum* (Buckley) Britton (38%), and *D. lanuginosum* (Michx.) Nicholson (25%), are rare or absent in our study region. Species commonly documented in northeastern Mesophytic Forests, but absent from the species lists reviewed for southeastern sites, included *Actaea rubra*, *Hepatica americana*, and *Polygonatum pubescens* (each cited in 43% of northeastern studies). In a comparison of northeastern and midwestern studies, 122 species were cited two or more times overall, and of these, 73% were cited in both regions. Several herbaceous taxa noted frequently in the Midwest, such as *Phlox divaricata* L. and *Anemone quinquefolia* L. (both cited in 67% of midwestern studies), are not commonly found at Mesophytic Forest sites in the Northeast, although *A. quinquefolia* does occur in the region.

DISCUSSION

While Rich Mesic Forests are well known to botanists and ecologists in the Northeast and are of considerable conservation interest due to their high species richness and associated rare species, few studies have investigated vegetation variation in relation to environment across multiple sites in Northeastern RMF. The results of this study provide a framework for assessing examples of RMF in the Northeast and a basis for comparison with Mesophytic Forests throughout eastern North America. This research identifies two dominant environmental gradients associated with RMF vegetation patterns in western Massachusetts: (1) variation in soil nutrient status (e.g., Ca concentration and pH), and (2) variation in physiography and associated environmental gradients (e.g., slope, bedrock exposure, and solar insolation).

Vegetation variation and soil fertility. The association of Mesophytic Forest vegetation with nutrient-rich, moderately acidic to circumneutral soils with high cation concentrations has been documented previously at other sites in the Northeast (e.g., Balter and Loeb 1983; Nault and Gagnon 1988), the Southeast (e.g., Graves and Monk 1982; Rawinski et al. 1996; Rheinhardt and Ware 1984), and the Midwest (e.g., Curtis 1959; Woods 2000; Zak et al. 1986). Further, in many locations a close association has been noted between these distinctive edaphic conditions and underlying calcareous bedrock (e.g., Balter and Loeb 1983; Graves and Monk 1982; Nault and Gagnon 1988).

In the Northeast, the influence of soil nutrient status and pH on RMF vegetation may be visualized as a gradient from sites with vegetation approximating more widespread northern or transition hardwoods vegetation on acidic, calcium-poor soils to nutrient-rich, “eutrophic” sites with RMF vegetation that is highly differentiated from forest vegetation in the surrounding landscape (Rawinski 1992; Siccama and Bormann 1970). While all plots for this study were located in forest vegetation including some RMF indicator species, the dominant vegetation on soils with the lowest pH and cation concentrations (i.e., Subtype 1A of ADP) is similar in species composition and structure to typical northern hardwoods forest vegetation, which contrasts strongly with RMF vegetation on nutrient-rich, mull soils (e.g., AAC and Subtype 1B of ADP). Comparison with soils data from studies across a range of northeastern forest types confirms that RMF and related *Acer saccharum*-dominated forest vegetation typically occurs at the upper end of a regional soil fertility gradient, exhibiting high soil cation concentrations and pH relative to other forest vegetation in the Northeast (Table 8; Siccama and Bormann 1970).

The unique edaphic conditions of RMF sites in the study area are due in large part to the calcareous influence of the underlying bedrock, which includes occasional marble interbeds or amphibolite (Chidester et al. 1967; Hatch et al. 1970; Segerstrom 1956). As this bedrock weathers, calcium (Ca^{2+}) and magnesium (Mg^{2+}) cations are released into the soil solution, displacing exchangeable hydrogen (H^+) and aluminum (Al^{3+}) ions on soil colloids, and increasing soil pH and nutrient availability in the process (Brady and Weil 1999). Colluvial processes in the lower slope and concave landscape positions where many RMF sites are located may also lead to increased soil pH and nutrient enrichment (Fisher and Binkley 2000; Thompson and Sorenson 2000).

The nutrient cycling characteristics of plant species associated with RMF may further enhance soil nutrient status. For instance, soil pH and cation concentrations may be elevated by the “nutrient pumping” ability of typical RMF tree species, such as *Acer saccharum*, *Fraxinus americana*, and *Tilia americana*, which can increase surface soil pH, Ca^{2+} , and K^+ concentrations through uptake of soil nutrients at depth and the production of readily degradable, high-nutrient leaf litter (Curtis 1959; Dijkstra and Smits 2002; Finzi et al. 1998a). Responding to the mesic, circumneutral soil conditions and high quality of plant litter, soil fauna and microflora may be abundant at RMF sites, leading to the rapid decomposition of leaf litter, the enhancement of soil structure and aeration, and development of deep, organic-rich A horizons typical of

mull soils (Curtis 1959; Perry 1994; Ponge et al. 1997). These environmental conditions likely result in greater nitrogen (N) availability for plants due to elevated rates of N mineralization and nitrification in RMF soils, as has been documented in forests dominated by *A. saccharum* and *F. americana* (Finzi et al. 1998b; Zak et al. 1986) and for sites with higher soil pH (Goodale and Aber 2001).

The differentiation of RMF from typical northern hardwoods vegetation with increasing soil fertility results from: (1) the occurrence of species exhibiting highly restricted distributions associated with nutrient-rich, calcareous soil conditions (e.g., *Athyrium pycnocarpon*, *Dryopteris goldiana*); (2) increased herbaceous layer cover, apparently as a result of the greater number of stems present per unit area and possibly the larger size of individual plants and species associated with mesic, nutrient-rich soils; and (3) increased species richness due to the accumulation of characteristic RMF taxa in addition to more widespread forest plant species. As a result of the later, the flora of RMF includes woodland generalists such as *Aster divaricatus*, *Polygonatum pubescens*, and *Smilacina racemosa*, as well as characteristic RMF taxa such as *Carex plantaginea*, *Allium tricoccum*, and *Hepatica acutiloba* (cf. Smith 1995). This gradient of species richness is most apparent in the comparison of subtypes within ADP, where the differentiation of Subtype 1B vegetation on nutrient-rich soils from Subtype 1A vegetation on poorer soils is driven primarily by the addition of species in Subtype 1B. Twenty-four species showed significantly higher frequency or cover in Subtype 1B, while only 3 species were significantly associated with Subtype 1A. Amongst the herb layer taxa associated with Subtype 1B are species such as *D. goldiana*, *C. plantaginea*, and *Matteuccia struthiopteris*, which are considered to be characteristic of high-nutrient soil conditions (Rawinski 1992). In contrast, of the two herbaceous species significantly associated with Subtype 1A, *Viola blanda* and *V. rotundifolia*, the later may be considered an indicator of lower nutrient conditions (Rawinski 1992; Thompson and Sorenson 2000).

The positive association between higher soil cation concentrations (e.g., Ca^{2+} , Mg^{2+}) or soil pH and species richness documented for ADP vegetation in this study has been noted elsewhere in the forests of eastern North America (Beals and Cope 1964; Christensen and Peet 1984; Greer et al. 1997; Peet et al. 2003; Searcy et al. 2003; Siccama and Bormann 1970), as well as in some European temperate deciduous forests (Borchsenius et al. 2004; Chytry et al. 2003). As many temperate forest ecosystems are nutrient limited (Fisher and Binkley 2000; Muller 2003), and increased soil cation concentrations and pH result in greater nutrient

Table 8. Selected chemical characteristics of mineral soils associated with various bedrock and forest vegetation types in the Northeast. Forest types are characterized by the dominant and codominant tree species noted in each study; RMF vegetation types described in the present study are indicated in bold type. Studies are presented in a relative ranking by soil pH, from circumneutral to strongly acidic. Sample sizes and soil sampling depths vary somewhat between studies, however methods of chemical analyses are generally comparable and the data presented are suitable for general comparison of surface soil chemical characteristics. Values presented are means; exchangeable cation concentrations are in ppm; missing data are indicated by —.

Dominant and Codominant	Location	Bedrock	Soil pH	Ca	K	Mg	Study
Canopy spp.							
<i>Acer saccharum-Fraxinus americana</i>	Gatineau Park, southern Quebec	Potassic aplite with calcium carbonate	6.4	3250	86	—	Nault and Gagnon 1988, 1993
<i>Acer saccharum-Tilia americana-Fraxinus americana</i>	Northern NJ and southeastern NY	Calciteic and dolomitic limestone	6.4	1079	54	101	Balter and Loeb 1983
RMF – ACC Type; <i>Acer saccharum-Fraxinus americana-Carya cordiformis</i>	Franklin Co. and Hampshire Co., MA	Schists with calcareous influence	5.2	1711	69	82	Present study
RMF – ADP Type, Subtype 1B; <i>Acer saccharum-Fraxinus americana</i>	Franklin Co. and Hampshire Co., MA	Schists with calcareous influence	5.1	1539	62	80	Present study
<i>Acer saccharum-Quercus rubra-Quercus prinus</i>	Holyoke Range - south slope, Hampshire Co., MA	Basalt	5.0	2454	159	264	Searcy et al. 2003
<i>Quercus rubra-Tsuga canadensis-Betula lenta-Acer saccharum</i>	Holyoke Range - north slope, Hampshire Co., MA	Basalt	4.7	2306	215	280	Searcy et al. 2003
<i>Quercus prinus-Quercus rubra</i>	Cary Arboretum, Dutchess Co., Hudson Valley, NY	Slates and shales	4.7	540	117	59	Giltzenstein et al. 1990
RMF – ADP Type, Subtype 1A; <i>Acer saccharum-Fraxinus americana</i>	Franklin Co. and Hampshire Co., MA	Schists with calcareous influence	4.6	701	46	53	Present study

Table 8. Continued.

Dominant and Codominant	Location	Bedrock	Soil pH	Ca	K	Mg	Study
<i>Quercus velutina-Acer rubrum-Carya glabra-Quercus alba</i>	Cary Arboretum, Dutchess Co., Hudson Valley, NY	Slates and shales	4.6	391	118	48	Glitzenstein et al. 1990
<i>Acer rubrum-Acer saccharum-Pinus strobus</i>	Cary Arboretum, Dutchess Co., Hudson Valley, NY	Slates and shales	4.5	635	122	69	Glitzenstein et al. 1990
<i>Acer rubrum-Betula lenta-Quercus prinus-Quercus rubra</i>	Northern NJ and southeastern NY	Gneiss	4.5	45	41	9	Balter and Loeb 1983
<i>Quercus coccinea-Quercus ilicifolia-Pinus rigida</i>	Montague Sand Plain, Franklin Co., MA	Outwash delta sand plain; bedrock at depth	4.5	18	26	6	Motzkin et al. 1996
<i>Acer saccharum-Fagus grandifolia-Betula alleghaniensis</i>	Hubbard Brook Experimental Forest, Grafton Co., NH	Gneiss	< 4.5	82	16	6	Whittaker et al. 1979
<i>Acer saccharum-Fagus grandifolia-Betula alleghaniensis</i>	Chittenden Co., VT	Schist	4.2	1139	95	100	Siccama 1968
<i>Pinus strobus-Betula lenta-Betula alleghaniensis-Tsuga canadensis</i>	Harvard Forest LTER, Worcester Co., MA	Gneiss and schist	4.2	38	—	16	Motzkin et al. 1999
<i>Quercus rubra-Betula lenta-Tsuga canadensis</i>	Holyoke Range - north slope, Hampshire Co., MA	Arkose sandstone	4.0	563	137	100	Searcy et al. 2003
<i>Quercus rubra-Quercus prinus-Acer rubrum</i>	Holyoke Range - south slope, Hampshire Co., MA	Arkose sandstone	3.9	372	126	75	Searcy et al. 2003
<i>Betula papyrifera-Picea rubens-Betula alleghaniensis</i>	Camels Hump, Chittenden Co., VT	Schist	3.9	138	125	67	Siccama 1968
<i>Abies balsamea-Picea rubens</i>	Camels Hump, Chittenden Co., VT	Schist	3.8	91	89	55	Siccama 1968

availability for plants (Brady and Weil 1999), this pattern is consistent with the positive monotonic or unimodal correlation found between indices of productivity and species richness in many ecosystems (Begon et al. 1996; Rosenzweig and Abramsky 1993). Elevated soil cation concentrations and pH may result in increased N availability for plants (Finzi et al. 1998b; Goodale and Aber 2001), potentially supporting higher rates of establishment and growth for many herbaceous taxa, including typical RMF species and woodland generalists (cf. Peet et al. 2003). While N availability was not directly measured in this study, previous research has documented a positive relationship between rates of potential N mineralization and nitrification and the occurrence of species-rich herb layer vegetation in *Acer saccharum*-dominated forests in Michigan (Zak et al. 1986). In the context of forests in the Northeast, it is likely that the favorable growing environment for plants engendered by greater nutrient availability in the soils of RMF sites relative to other forest types on more acidic, nutrient-poor soils (e.g., transition or northern hardwoods vegetation) results in increased herb layer cover and species richness. Greater resource availability may simply allow for greater numbers of individuals to occupy a given area, which, barring strong competitive interactions between species, is likely to result in increased numbers of species present per unit area (Begon et al. 1996).

Nevertheless, the conspicuous restriction of many RMF indicator taxa to nutrient-rich, circumneutral soils also suggests that a considerable number of these species may lack ecophysiological characteristics allowing them to establish, survive, and reproduce on the more acidic forest soils that predominate across much of the Northeast. These species' distribution patterns may relate to limited tolerance of increased Al concentration and toxicity in soils at low pH, which can inhibit uptake of essential ions (e.g., Ca^{2+} , Mg^{2+} , phosphate) and interfere with root growth; similarly, increased H^+ concentration at low pH may damage root cells and impair uptake of nutrients (Lee 1999; Marschner 1991; Tyler 2003). Rates of nitrogen cycling and the relative importance of mineralization and nitrification in yielding plant-available N (e.g., NO_3^- vs. NH_4^+) may also vary strongly among sites dependent upon soil chemical characteristics and species composition of the forest canopy (Finzi et al. 1998b; Tyler 2003; Zak et al. 1986); as forest herbs likely vary in their nitrogen-use efficiency and in their ability to uptake and utilize differing forms of N (Lee 1999; Neufeld and Young 2003; Rothstein and Zak 2001), species distributions may relate in part to variation in these site soil characteristics.

In addition to the potential for elevated soil nutrients and pH to influence plant performance at RMF sites, the rapid decomposition of

leaf litter and reduced or absent O layer typical of mull soils (Curtis 1959; Perry 1994) may also allow for greater rates of seedling establishment. Leaf litter may act as a physical or chemical limiting factor to the germination and growth of seedlings (Baskin and Baskin 2001; Beatty 2003), and the depth of leaf litter in temperate deciduous forests has been shown to relate to the distribution of some ground layer herbaceous species (Sydes and Grime 1981). Consistent with these observations, litter removal experiments in Northeastern deciduous forests have resulted in increased species richness at the plot scale (Beatty 2003).

Beyond local environmental conditions and species interactions, regional factors are increasingly recognized as important influences on local species richness in many communities (Caley and Schluter 1997; Cornell and Lawton 1992; Ricklefs and Schluter 1993). Specifically, the relative sizes of species pools associated with different vegetation types in a region may play an important role in driving plot-scale species richness patterns in plant communities (Eriksson 1993; Partel et al. 1996; Zobel et al. 1998). While increased nutrient availability in the soils of RMF sites may allow for greater numbers of individuals or ramets to grow per unit area, it is the total number of species present in the region that are adapted to survive in RMF habitat (i.e., the regional species pool for RMF; Dupre 2000; Partel et al. 1996), which may be a strong determinant of how many taxa are actually present at a given site or plot. As noted in this study and by previous researchers (Braun 1950; Parnall 1998), the distinctive environmental conditions of northeastern RMF sites provide habitat suitable for many forest herb species typical of the Mesophytic Forests of the southern Appalachians. Southeastern Mesophytic Forests are widely recognized as having a large pool of ground-layer herbaceous plant species relative to other forest types in eastern North America (Braun 1950; Peet et al. 2003; Whittaker 1965); consequently, high species richness at the local or plot scale in RMF and other Mesophytic Forest types, may relate directly to the larger regional pool of plant species which can potentially inhabit these sites (Peet et al. 2003).

Vegetation variation and site physiography. In mountainous or hilly terrain, physiographic characteristics of a site, such as slope and aspect, can be critical determinants of insolation, temperature, and moisture availability (Campbell 1977; Cantlon 1953; Lipscomb and Nilsen 1990). Numerous studies have documented that these environmental factors may be key controls on the distribution and abundance of many plant species (e.g., Cantlon 1953; Olivero and Hix 1998; Seischab 1985; Whittaker 1956).

In RMF, variation in physiography and correlated environmental factors (e.g., insolation levels) emerges as a key driver of vegetation variation among sites with otherwise similar, nutrient-rich edaphic conditions. This effect is suggested in the ordination, where AAC and ADP are primarily differentiated along Axis 1, which is highly correlated with solar insolation and slope, but not with edaphic variables such as soil pH, Ca, or C:N ratio. The steeper slopes and more southerly aspects of plots in AAC result in significantly higher solar insolation levels than in ADP plots ($p < 0.001$). Increased insolation may have a variety of direct physiological effects on plants (e.g., higher photosynthetic and evapotranspiration rates; Neufeld and Young 2003), as well as indirect effects on environmental conditions (e.g., the timing of snowmelt), which in turn may influence species performance and distribution. As an apparent consequence of variation in insolation, species typical of cool, mesic northern hardwoods forest (e.g., *Acer pensylvanicum*, *Claytonia caroliniana*, *Dryopteris intermedia*, *Tiarella cordifolia*) are associated with ADP sites, where insolation levels are low (Reschke 1990; Thompson and Sorenson 2000; Weatherbee 1996). In contrast, higher insolation levels in AAC apparently favor species tolerant of warmer and drier conditions. For instance, the predominance of woodland sedges, grasses, and *Solidago* spp. in AAC vegetation (e.g., *Carex appalachica*, *C. communis*, *Oryzopsis racemosa*, *S. caesia*) suggests summer vegetation adapted to warmer and drier conditions (cf. Cantlon 1953). Similarly, *Acer nigrum* and *Cardamine concatenata*, two species near their northeastern range limits in the region, were documented solely in AAC vegetation.

In addition to variation in temperature and moisture levels, increased spring light levels and earlier snowmelt may strongly influence some ephemerals, as these species concentrate their entire annual photosynthetic activity into a brief period prior to canopy leaf-out (Neufeld and Young 2003). The extensive colonies of *Allium tricoccum* in AAC (100% frequency, 10.6% mean cover) suggest that high insolation and nutrient-rich soils may interact “synergistically” for the species, as has been documented for *Claytonia virginica*, another spring ephemeral species (Eickmeier and Schussler 1993). The lower cover of *A. tricoccum* in Subtype 1B plots (3.4%; $p = 0.020$), where edaphic conditions are comparable to AAC, but insolation levels are lower, further suggests the importance of high spring light levels for this species. The association between *A. tricoccum* abundance and high insolation is consistent with observations of populations of its European congener *A. ursinum* L., also a forest species, in which plants growing under high-light conditions exhibited five and a half times greater bulb

biomass than plants growing on north-facing slopes with low light (Ernst 1979). Similarly, *Sanguinaria canadensis*, a species that responds vigorously to high light levels with increased growth and seed production (Marino et al. 1997; Schemske 1978), occurs at high frequency in AAC (70%), but is absent from ADP vegetation.

The combination of frequent, small bedrock exposures (often of calcareous rock) and southerly aspect in AAC also provides a unique habitat for some taxa typical of the Southern Calcareous Cliff Community described by Weatherbee (1996) for Berkshire County, MA. Species such as *Saxifraga virginiensis*, *Asplenium trichomanes*, *Cystopteris fragilis*, and *C. bulbifera* are often found on bedrock outcrops and boulders in AAC, further differentiating the type from ADP vegetation.

Regional variation of Mesophytic Forests. The comparison of forest canopy and herbaceous layers of Mesophytic Forests throughout eastern North America indicates a high degree of constancy in species composition across geographic regions (cf. Braun 1950; Curtis 1959; Parnall 1998). Dominant herb species in RMF of the Northeast, such as *Caulophyllum thalictroides*, *Allium tricoccum*, and *Asarum canadense*, are important in similar Mesophytic Forest communities throughout eastern North America, reinforcing the categorization of RMF as a northeastern variant of the Mesophytic Forest community type (Braun 1950; Gauch and Stone 1979; Parnall 1998). In one striking example, over 50% of the common herb layer taxa noted at a Mesophytic Forest site in Georgia (Graves and Monk 1982) have also been documented at RMF sites over 1000 km to the north in western Massachusetts (this study; Bellemare et al. 2002); these include typical northeastern RMF species such as *C. thalictroides*, *Carex plantaginea*, *Athyrium pycnocarpon*, and *Osmorhiza claytonii*. Recent work by MacDougal (2001) has even documented several of these taxa in association with areas of rich deciduous forest at the edge of the boreal forest zone in New Brunswick. Nevertheless, regional and latitudinal trends in species composition and diversity in Mesophytic Forests should not be overlooked, with notable differences in species composition and richness of the forest canopy when moving from the southern Appalachians to the north (Braun 1950; Currie and Paquin 1987).

Comparisons between the present study and the work of Curtis (1959) and Rogers (1982) in the upper Midwest also document compositional similarities between geographically distant northern examples of Mesophytic Forest. Curtis distinguishes “northern” and “southern” mesic types in the Mesophytic Forests of Wisconsin, while Rogers refers

to these types as “northern” and “central” mesophytic hardwoods. Several taxa noted by these authors as indicators of the two types in the Midwest exhibit associations with the AAC and ADP vegetation types described in our study. For example, species typical of the “southern” or “central” Mesophytic Forests, such as *Cardamine concatenata*, *Circaea lutetiana*, *Hepatica acutiloba*, and *Oryzopsis racemosa*, tend to be associated with AAC in this study, whereas “northern” species, such as *Claytonia caroliniana*, *Cardamine diphylla*, *Maianthemum canadense*, and *Uvularia sessilifolia*, are associated with ADP. Similarly, tree species typical of the “northern” type in Wisconsin, such as *Fagus grandifolia* and *Betula alleghaniensis* (Curtis 1959), occur solely in the canopy of ADP vegetation in western Massachusetts. In the upper Midwest, this pattern occurs on a larger geographic scale along south-north and east-west gradients, evidently in response to climatic and edaphic variation (Curtis 1959; Rogers 1982). In western Massachusetts, local variation in physiography and edaphic conditions leads to the development of comparable patterns in RMF vegetation on a local scale, including intergradation among RMF types and subtypes at larger RMF sites.

Conservation implications. The results of this study suggest that the AAC vegetation type of RMF is restricted in the region due to its strong association with a unique, spatially limited physiographic setting: relatively steep, southeast to south-facing, concave slopes with mesic, calcareous soils and frequent bedrock outcrops. These distinctive physiographic and geologic characteristics may allow for effective use of readily available GIS data layers in identifying potential AAC sites across the region (B. Compton and K. Rolih, Landscape Ecology Program, Dept. Natural Resources, Univ. Massachusetts, Amherst, pers. comm.). The spatial extent of Subtype 1B vegetation of the ADP Type may also be limited due to its association with relatively uncommon nutrient-rich, calcareous soils; however, the physiographic correlates of this type are less distinctive, and identification of sites *a priori* using GIS may be less effective. In addition, the fertile soils and more agriculturally suitable terrain of Subtype 1B may have resulted in a substantial proportion of this RMF subtype being converted to agriculture in the 19th century; as a consequence, many prospective Subtype 1B sites may at present be occupied by post-agricultural, secondary forests with reduced herbaceous layers (Bellemare et al. 2002). Subtype 1A vegetation is apparently more widespread, as it may develop in a variety of physiographic settings where mesic soils become enriched by colluvial accumulation of nutrients or where there is a moderate calcareous influence from local bedrock.

From the perspective of biodiversity conservation, AAC vegetation should be a priority for protection, as it is of limited extent and may provide habitat for rare plant species. Several regionally rare plant species documented during the course of this research, including *Carex hitchcockiana*, *Hydrophyllum canadense* L., and *Milium effusum* L., were found at sites with AAC vegetation. While characterized by fewer rare taxa, Subtype 1B of ADP supports species-rich forest vegetation worthy of conservation efforts. Conservation decisions regarding RMF sites must balance the desire to identify and conserve species-rich variants of RMF that may have been reduced in extent by past human disturbance (i.e., ADP Subtype 1B vegetation), with the need to protect unusual sites and rare plant species (i.e., AAC vegetation).

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LITERATURE CITED

- ANONYMOUS. 1995. Soil survey of Hampden and Hampshire Counties, western part, Massachusetts. U.S. Dept. Agriculture, Natural Resources Conservation Service, Washington, DC.
- ANONYMOUS. 1998. Standard test method for particle size analysis of soils. ASTM D422-63, American Society for Testing and Materials, Vol. 04.08. ASTM, West Conshohocken, PA.
- BALTER, H. AND R. E. LOEB. 1983. Arboreal relationships on limestone and gneiss in northern New Jersey and southeastern New York. *Bull. Torrey Bot. Club* 110: 370–379.
- BASKIN, C. C. AND J. M. BASKIN. 2001. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, CA.
- BEALS, E. W. AND J. B. COPE. 1964. Vegetation and soils in an eastern Indiana woods. *Ecology* 45: 777–792.

- BEATTY, S. W. 2003. Habitat heterogeneity and maintenance of species in understory communities, pp. 177–197. *In*: F. S. Gilliam and M. R. Roberts, eds., *The Herbaceous Layer in Forests of Eastern North America*. Oxford Univ. Press, Oxford, U.K.
- BEGON, M., J. L. HARPER, AND C. R. TOWNSEND. 1996. *Ecology*, 3rd ed. Blackwell Science, Oxford, U.K.
- BELLEMARE, J., G. MOTZKIN, AND D. R. FOSTER. 2002. Legacies of the agricultural past in the forested present: An assessment of historical land-use effects on rich mesic forests. *J. Biogeogr.* 29: 1401–1420.
- BORCHSENIUS, F., P. K. NIELSEN, AND J. LAWESSON. 2004. Vegetation structure and diversity of an ancient temperate deciduous forest in SW Denmark. *Pl. Ecol.* 175: 121–135.
- BRADY, N. C. AND R. R. WEIL. 1999. *The Nature and Properties of Soils*, 12th ed. Prentice Hall, Upper Saddle River, NJ.
- BRATTON, S. P., J. R. HAPEMAN, AND A. R. MAST. 1994. The lower Susquehanna River gorge and floodplain (U.S.A.) as a riparian refugium for vernal, forest-floor herbs. *Conservation Biol.* 8: 1069–1077.
- BRAUN, L. 1950. *Deciduous Forests of Eastern North America*. Blakiston Co., Philadelphia, PA.
- CAIN, S. A. 1943. The tertiary character of the cove hardwood forests of the Great Smoky Mountains National Park. *Bull. Torrey Bot. Club* 70: 213–235.
- CALEY, M. J. AND D. SCHLUTER. 1997. The relationship between local and regional diversity. *Ecology* 78: 70–80.
- CAMPBELL, G. S. 1977. *An Introduction to Environmental Biophysics*. Springer-Verlag, New York.
- CANTLON, J. E. 1953. Vegetation and microclimates on north and south slopes of Cushtunk Mountain, New Jersey. *Ecol. Monogr.* 23: 241–270.
- CHIDESTER, A. H., N. L. HATCH, JR., P. H. OSBERG, S. A. NORTON, AND J. H. HARTSHORN. 1967. *Geologic map of the Rowe quadrangle, Massachusetts-Vermont*. Dept. Interior, U.S. Geological Survey, Washington, DC.
- CHRISTENSEN, N. L. AND R. K. PEET. 1984. Convergence during secondary forest succession. *J. Ecol.* 72: 25–36.
- CHYTRY, M., L. TICHY, AND J. ROLESEK. 2003. Local and regional patterns of species richness in central European vegetation types along the pH/calcium gradient. *Folia Geobot. Phytotax.* 38: 429–442.
- CORNELL, H. V. AND J. H. LAWTON. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: A theoretical perspective. *J. Animal Ecol.* 61: 1–12.
- CURRIE, D. J. AND V. PAQUIN. 1987. Large-scale biogeographical patterns of species richness of trees. *Nature* 329: 326–327.
- CURTIS, J. T. 1959. *The Vegetation of Wisconsin*. Univ. Wisconsin Press, Madison, WI.
- DAUBENMIRE, R. F. 1936. The “Big Woods” of Minnesota: Its structure, and relation to climate, fire, and soils. *Ecol. Monogr.* 6: 233–268.
- DIJKSTRA, F. A. AND M. M. SMITS. 2002. Tree species effects on calcium cycling: The role of calcium uptake in deep soils. *Ecosystems* 5: 385–389.
- DUFFY, D. C. AND A. J. MEIER. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? *Conservation Biol.* 6: 196–201.
- DUPRE, C. 2000. How to determine a regional species pool: A study in two Swedish regions. *Oikos* 89: 128–136.

- EGGLER, W. A. 1938. The maple-basswood forest type in Washburn County, Wisconsin. *Ecology* 19: 243–263.
- EICKMEIER, W. G. AND E. E. SCHUSSLER. 1993. Responses of the spring ephemeral *Claytonia virginica* L. to light and nutrient manipulations and implications for the “vernal-dam” hypothesis. *Bull. Torrey Bot. Club* 120: 157–165.
- ERIKSSON, O. 1993. The species-pool hypothesis and plant community diversity. *Oikos* 68: 371–374.
- ERNST, W. H. O. 1979. Population biology of *Allium ursinum* in northern Germany. *J. Ecol.* 67: 347–362.
- FEDERER, C. A., D. E. TURCOTTE, AND C. T. SMITH. 1993. The organic fraction—bulk density relationship and the expression of nutrient content in forest soils. *Canad. J. Forest Res.* 23: 1026–1032.
- FINZI, A. C., C. D. CANHAM, AND N. VAN BREEMEN. 1998a. Canopy tree-soil interactions within temperate forests: Species effects on pH and cations. *Ecol. Applic.* 8: 447–454.
- , N. VAN BREEMEN, AND C. D. CANHAM. 1998b. Canopy tree-soil interactions within temperate forests: Species effects on soil carbon and nitrogen. *Ecol. Applic.* 8: 440–446.
- FISHER, R. F. AND D. BINKLEY. 2000. *Ecology and Management of Forest Soils*, 3rd ed. John Wiley and Sons, New York.
- GAUCH, H. G., JR. AND E. L. STONE. 1979. Vegetation and soil pattern in a mesophytic forest at Ithaca, New York. *Amer. Midl. Naturalist* 102: 332–345.
- GLEASON, H. A. AND A. CRONQUIST. 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, 2nd ed. The New York Botanical Garden, New York.
- GLITZENSTEIN, J. S., C. D. CANHAM, M. J. McDONNELL, AND D. R. STRENG. 1990. Effects of environment and land use history on upland forests of the Cary Arboretum, Hudson Valley, New York. *Bull. Torrey Bot. Club* 117: 106–122.
- GOODALE, C. L. AND J. D. ABER. 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. *Ecol. Applic.* 11: 253–267.
- GRAVES, J. H. AND C. D. MONK. 1982. Herb-soil relationships on a lower north slope over marble. *Bull. Torrey Bot. Club* 109: 500–507.
- GREER, G. K., R. M. LLOYD, AND B. C. MCCARTHY. 1997. Factors influencing the distribution of pteridophytes in a southeastern Ohio hardwood forest. *J. Torrey Bot. Soc.* 124: 11–21.
- GREGORICH, E. G., L. W. TURCHENEK, M. R. CARTER, AND D. A. ANGERS. 2002. *Soil and environmental science dictionary*. CRC Press, Boca Raton, FL.
- GREIG-SMITH, P. 1983. *Quantitative Plant Ecology*, 3rd ed. Blackwell Scientific Publications, Oxford, U.K.
- HANDEL, S. N., S. B. FISCH, AND G. E. SCHATZ. 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. *Bull. Torrey Bot. Club* 108: 430–437.
- HATCH, N. L., JR., S. A. NORTON, AND R. G. CLARK, JR. 1970. Geologic map of the Chester quadrangle, Hampden and Hampshire Counties, Massachusetts. Dept. Interior, U.S. Geological Survey, Washington, DC.

- HILL, M. O. 1979. DECORANA—A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and Systematics, Cornell Univ., Ithaca, NY.
- KUCERA, C. L. 1952. An ecological study of a hardwood forest area in central Iowa. Ecol. Monogr. 22: 283–299.
- LEE, J. A. 1999. The calcicole-calcifuge problem revisited. Advances Bot. Res. 29: 1–30.
- LIPSCOMB, M. V. AND E. T. NILSEN. 1990. Environmental and physiological factors influencing the natural distribution of evergreen and deciduous ericaceous shrubs on northeast- and southwest-facing slopes of the southern Appalachian Mountains. II. Water relations. Amer. J. Bot. 77: 517–526.
- MACDOUGAL, A. 2001. Conservation status of Saint John River Valley Hardwood Forest in western New Brunswick. Rhodora 103: 47–70.
- MARINO, P. C., R. M. EISENBERG, AND H. V. CORNELL. 1997. Influence of sunlight and soil nutrients on clonal growth and sexual reproduction of the understory perennial herb *Sanguinaria canadensis* L. J. Torrey Bot. Soc. 124: 219–227.
- MARKS, J. B. 1942. Land use and plant succession in Coon Valley, Wisconsin. Ecol. Monogr. 12: 113–133.
- MARSCHNER, H. 1991. Mechanisms of adaptation of plants to acid soils. Pl. & Soil 134: 1–20.
- MASSGIS. 2004. Bedrock Lithology Shapefile. MassGIS, Commonwealth of Massachusetts. Executive Office of Environmental Affairs. Boston, MA. Website (<http://www.mass.gov/mgis/bedlith.htm>).
- MATLACK, G. R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology 75: 1491–1502.
- MCCUNE, B. AND M. J. MEFFORD. 1999. PC-ORD: Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, OR.
- MCLEAN, E. O. 1982. Soil pH and lime requirement, pp. 199–223. In: A. L. Page, R. H. Miller, and D. R. Keeney, eds., Methods of Soil Analysis. Part 2 – Chemical and Microbiological Properties, 2nd ed. American Society of Agronomy, Madison, WI.
- MCNAB, W. H. 1989. Terrain Shape Index: Quantifying effect of minor landforms on tree height. Forest Sci. 35: 91–104.
- MEHLICH, A. 1984. Mehlich 3 soil test extractant: A modification of the Mehlich 2 extractant. Commun. Soil Sci. Pl. Analysis 15: 1409–1416.
- MOTT, J. R. AND D. C. FULLER. 1967. Soil survey of Franklin County, Massachusetts. U.S. Dept. Agriculture, Soil Conservation Service, Washington, DC.
- MOTZKIN, G., D. FOSTER, A. ALLEN, J. HARROD, AND R. BOONE. 1996. Controlling site to evaluate history: Vegetation patterns of a New England sand plain. Ecol. Monogr. 66: 345–365.
- , P. WILSON, D. R. FOSTER, AND A. ALLEN. 1999. Vegetation patterns in heterogeneous landscapes: The importance of history and environment. J. Veg. Sci. 10: 903–920.
- MULLER, R. N. 2003. Nutrient relations of the herbaceous layer in deciduous forest ecosystems, pp. 15–37. In: F. S. Gilliam and M. R. Roberts, eds., The Herbaceous Layer in Forests of Eastern North America. Oxford Univ. Press, Oxford, U.K.

- NAULT, A. AND D. GAGNON. 1988. Seasonal biomass and nutrient allocation patterns in wild leek (*Allium tricoccum* Ait.), a spring geophyte. *Bull. Torrey Bot. Club* 115: 45–54.
- AND ———. 1993. Ramet demography of *Allium tricoccum*, a spring ephemeral, perennial forest herb. *J. Ecol.* 81: 101–119.
- NEUFELD, H. S. AND D. R. YOUNG. 2003. Ecophysiology of the herbaceous layer in temperate deciduous forests, pp. 38–90. *In*: F. S. Gilliam and M. R. Roberts, eds., *The Herbaceous Layer in Forests of Eastern North America*. Oxford Univ. Press, Oxford, U.K.
- OLIVERO, A. M. AND D. M. HIX. 1998. Influence of aspect and stand age on ground flora of southeastern Ohio forest ecosystems. *Pl. Ecol.* 139: 177–187.
- OLLINGER, S. V., J. D. ABER, C. A. FEDERER, G. M. LOVETT, AND J. ELLIS. 1995. Modeling physical and chemical climatic variables across the northeastern U.S. for a Geographic Information System. General Technical Report No. NE-191, U.S. Dept. Agriculture, Forest Service, Washington, DC.
- PARNALL, R. 1998. Vegetation and land-use history of nine mesophytic forest stands in western Franklin County, Massachusetts. M.S. thesis, Connecticut College, New London, CT.
- PARTEL, M., M. ZOBEL, K. ZOBEL, AND E. VAN DER MAAREL. 1996. The species pool and its relation to species richness: Evidence from Estonian plant communities. *Oikos* 75: 111–117.
- PEARSON, S. M., A. B. SMITH, AND M. G. TURNER. 1998. Forest patch size, land use, and mesic forest herbs in the French Broad River Basin, North Carolina. *Castanea* 63: 382–395.
- PEET, R. K., J. D. FRIDLEY, AND J. M. GRAMLING. 2003. Variation in species richness and species pool size across a pH gradient in forests of the southern Blue Ridge Mountains. *Folia Geobot. Phytotax.* 38: 391–401.
- PERRY, D. A. 1994. *Forest Ecosystems*. Johns Hopkins Univ. Press, Baltimore, MD.
- PONGE, J. F., P. ARPIN, F. SONDAG, AND F. DELECOUR. 1997. Soil fauna and site assessment in beech stands of the Belgian Ardennes. *Canad. J. Forest Res.* 27: 2053–2064.
- RAWINSKI, T. J. 1992. A classification of Virginia's indigenous biotic communities: Vegetated terrestrial, palustrine, and estuarine community classes. Natural Heritage Technical Report No. 92-21, Virginia Dept. Conservation and Recreation, Div. Natural Heritage, Richmond, VA.
- ET AL. 1996. Plant communities and ecological land units of the Glenwood Ranger District, George Washington and Jefferson National Forests, Virginia. Natural Heritage Technical Report No. 96-20, Virginia Dept. Conservation and Recreation, Div. Natural Heritage, Richmond, VA.
- RESCHKE, C. 1990. *Ecological Communities of New York State*. New York Natural Heritage Program, New York State Dept. Environmental Conservation, Latham, NY.
- RHEINHARDT, R. D. AND S. A. WARE. 1984. The vegetation of the Balsam Mountains of southwest Virginia: A phytosociological study. *Bull. Torrey Bot. Club* 111: 287–300.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.
- RICKLEFS, R. E. AND D. SCHLUTER. 1993. Species diversity: Regional and historical influences, pp. 350–363. *In*: R. E. Ricklefs and D. Schluter, eds., *Species Diversity in Ecological Communities*. Univ. Chicago Press, Chicago, IL.

- ROGERS, R. S. 1982. Early spring herb communities in mesophytic forests of the Great Lakes region. *Ecology* 63: 1050–1063.
- ROSENZWEIG, M. L. AND Z. ABRAMSKY. 1993. How are diversity and productivity related, pp. 52–65. *In*: R. E. Ricklefs and D. Schluter, eds., *Species Diversity in Ecological Communities*. Univ. Chicago Press, Chicago, IL.
- ROTHSTEIN, D. E. AND D. R. ZAK. 2001. Relationships between plant nitrogen economy and life history in three deciduous-forest herbs. *J. Ecol.* 89: 385–394.
- SCHEMSKE, D. W. 1978. Sexual reproduction in an Illinois population of *Sanguinaria canadensis* L. *Amer. Midl. Naturalist* 100: 261–268.
- SEARCY, K., B. F. WILSON, AND J. H. FOWNES. 2003. Influence of bedrock and aspect on soils and plant distribution in the Holyoke Range, Massachusetts. *J. Torrey Bot. Soc.* 130: 158–169.
- SEGERSTROM, K. 1956. Bedrock geology of the Colrain quadrangle, Massachusetts-Vermont. Dept. Interior, U.S. Geological Survey, Washington, DC.
- SEISCHAB, F. K. 1985. An analysis of the Bristol Hills of New York. *Amer. Midl. Naturalist* 114: 77–83.
- SICCAMA, T. G. 1968. Altitudinal distribution of forest vegetation in relation to soil and climate on the slopes of the Green Mountains. Ph.D. dissertation, Univ. Vermont, Burlington, VT.
- AND F. H. BORMANN. 1970. The Hubbard Brook ecosystem study: Productivity, nutrients, and phytosociology of the herbaceous layer. *Ecol. Monogr.* 40: 389–402.
- SINGLETON, R., S. GARDESCU, P. L. MARKS, AND M. A. GEBER. 2001. Forest herb colonization of postagricultural forests in central New York State, USA. *J. Ecol.* 89: 325–338.
- SMITH, M. 1995. Community and edaphic analysis of upland northern hardwood communities, central Vermont, USA. *For. Ecol. Managem.* 72: 235–249.
- STORE, D. A. 1984. A simple high volume ashing procedure for determining soil organic matter. *Commun. Soil Sci. Pl. Analysis* 15: 79–772.
- SWAIN, P. C. AND J. B. KEARSLEY. 2000. Classification of the natural communities of Massachusetts (draft). Natural Heritage and Endangered Species Program, Massachusetts Div. Fisheries Wildlife, Westborough, MA.
- SYDES, C. AND J. P. GRIME. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. I. Field investigations. *J. Ecol.* 69: 237–248.
- THOMPSON, E. H. AND E. R. SORENSON. 2000. *Wetland, Woodland, Wildland: A Guide to the Natural Communities of Vermont*. University Press of New England, Hanover, NH.
- TYLER, G. 2003. Some ecophysiological and historical approaches to species richness and calcicole/calcifuge behaviour—contribution to a debate. *Folia Geobot. Phytotax.* 38: 419–428.
- VEZINA, P. E. AND M. M. GRANDTNER. 1965. Phenological observations of spring geophytes in Quebec. *Ecology* 46: 869–872.
- WEATHERBEE, P. 1996. *Flora of Berkshire County, Massachusetts*. The Berkshire Museum, Pittsfield, MA.
- AND G. E. CROW. 1992. Natural plant communities of Berkshire County, Massachusetts. *Rhodora* 94: 171–209.
- WESTVELD, M. 1956. Natural forest vegetation zones of New England. *J. Forest.* 54: 332–338.

- WHITTAKER, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26: 1–80.
- . 1965. Dominance and diversity in land plant communities. *Science* 147: 250–260.
- , G. E. LIKENS, F. H. BORMANN, J. S. EATON, AND T. G. SICCAMA. 1979. The Hubbard Brook ecosystem study: Forest nutrient cycling and element behavior. *Ecology* 60: 203–220.
- WILLIAMS, A. B. 1936. The composition and dynamics of a beech-maple climax community. *Ecol. Monogr.* 6: 317–408.
- WOODS, K. D. 2000. Dynamics in late-successional hemlock-hardwood forests over three decades. *Ecology* 81: 110–126.
- ZAK, D. R., K. S. PREGITZER, AND G. E. HOST. 1986. Landscape variation in nitrogen mineralization and nitrification. *Canad. J. Forest Res.* 16: 1258–1263.
- ZEN, E. 1983. Bedrock geologic map of Massachusetts. Map scale 1:250,000. Dept. Interior, U.S. Geological Survey, Washington, DC.
- ZOBEL, M., E. VAN DER MAAREL, AND C. DUPRE. 1998. Species pool: The concept, its determination and significance for community restoration. *Appl. Veg. Sci.* 1: 55–66.

APPENDIX 1

Studies included in the eastern North America Mesophytic Forest literature review, by region. Full citations are listed in Literature Cited section. Northeastern studies included: Bellemare et al. (this study) in Massachusetts; Handel et al. (1981) in New York; MacDougal (2001) in New Brunswick; Nault and Gagnon (1993) in Quebec; Singleton et al. (2001) in New York; Vezina and Grandtner (1965) in Quebec; Weatherbee (1996) in Massachusetts. Midwestern studies included: Beals and Cope (1964) in Indiana; Daubenmire (1936) in Minnesota; Egger (1938) in Wisconsin; Kucera (1952) in Iowa; Marks (1942) in Wisconsin; Williams (1936) in Ohio. Southeastern studies included: Bratton et al. (1994) in Pennsylvania and Maryland; Braun (1950) in the southern Appalachians; Cain (1943) in Tennessee and North Carolina; Graves and Monk (1982) in Georgia; Matlack (1994) in Delaware and Pennsylvania; Pearson et al. (1998) in North Carolina; Rawinski (1992) in Virginia; Whittaker (1956) in Tennessee and North Carolina.

APPENDIX 2

Vascular plant taxa documented in 36 Rich Mesic Forest plots in western Massachusetts. Values presented are percent frequency of occurrence across all plots in the herbaceous layer (all vascular plants ≤ 1 m in height), shrub layer (woody species > 1 m, < 2.5 cm DBH), and canopy and subcanopy (woody species > 1 m and > 2.5 cm DBH).

Taxon	Herbaceous Layer	Shrub Layer	Canopy and Subcanopy
LYCOPODIOPHYTA			
LYCOPODIACEAE			
<i>Lycopodium lucidulum</i> Michx.	8.3		
<i>Lycopodium obscurum</i> L.	2.8		
POLYPODIOPHYTA			
ADIANTACEAE			
<i>Adiantum pedatum</i> L.	77.8		
ASPLENIACEAE			
<i>Asplenium trichomanes</i> L.	8.3		
<i>Athyrium filix-femina</i> (L.) Roth	52.8		
<i>Athyrium pycnocarpon</i> (Sprengel) Tidestrom	22.2		
<i>Athyrium thelypteroides</i> (Michx.) Desv.	66.7		
<i>Cystopteris bulbifera</i> (L.) Bernh.	8.3		
<i>Cystopteris fragilis</i> (L.) Bernh.	44.4		
<i>Dryopteris carthusiana</i> (Villars) H. P. Fuchs	2.8		
<i>Dryopteris goldiana</i> (Hook.) A. Gray	30.6		
<i>Dryopteris intermedia</i> (Muhl.) A. Gray	69.4		
<i>Dryopteris marginalis</i> (L.) A. Gray	75.0		
<i>Polystichum acrostichoides</i> (Michx.) Schott	91.7		
<i>Thelypteris noveboracensis</i> (L.) Nieuwl.	13.9		
<i>Thelypteris phegopteris</i> (L.) Slosson	2.8		
DENNSTAEDTIACEAE			
<i>Dennstaedtia punctilobula</i> (Michx.) Moore	27.8		
ONOCLEACEAE			
<i>Matteuccia struthiopteris</i> Todaro	19.4		
<i>Onoclea sensibilis</i> L.	16.7		
OPHIOGLOSSACEAE			
<i>Botrychium lanceolatum</i> (S.G. Gmel.) Angström	5.6		
<i>Botrychium matricariaefolium</i> A. Braun	5.6		
<i>Botrychium virginianum</i> (L.) Swartz	30.6		
OSMUNDACEAE			
<i>Osmunda claytoniana</i> L.	8.3		

Appendix 2. Continued

Taxon	Herbaceous Layer	Shrub Layer	Canopy and Subcanopy
POLYPODIACEAE			
<i>Polypodium virginianum</i> L.	2.8		
PINOPHYTA			
PINACEAE			
<i>Picea rubens</i> Sarg.	2.8		
<i>Tsuga canadensis</i> (L.) Carrière		8.3	13.9
MAGNOLIOPHYTA – MAGNOLIOPSIDA			
ACERACEAE			
<i>Acer nigrum</i> Michx. f.	8.3	5.6	2.8
<i>Acer pensylvanicum</i> L.	52.8	52.8	36.1
<i>Acer rubrum</i> L.	11.1		2.8
<i>Acer saccharum</i> Marshall	100.0	88.9	100.0
<i>Acer spicatum</i> Lam.	30.6	11.1	5.6
ANACARDIACEAE			
<i>Rhus typhina</i> L.		2.8	2.8
<i>Toxicodendron radicans</i> (L.) Kuntze	8.3		
AQUIFOLIACEAE			
<i>Ilex verticillata</i> (L.) A. Gray	2.8		
ARALIACEAE			
<i>Aralia nudicaulis</i> L.	13.9		
<i>Aralia racemosa</i> L.	5.6		
<i>Panax quinquefolius</i> L.	25.0		
<i>Panax trifolius</i> L.	22.2		
ARISTOLOCHIACEAE			
<i>Asarum canadense</i> L.	63.9		
ASTERACEAE			
<i>Aster acuminatus</i> Michx.	19.4		
<i>Aster cordifolius</i> L.	19.4		
<i>Aster divaricatus</i> L.	91.7		
<i>Aster lanceolatus</i> Willd. or <i>A. lateriflorus</i> (L.) Britton	19.4		
<i>Aster macrophyllus</i> L.	2.8		
<i>Eupatorium rugosum</i> Houtt.	63.9		
<i>Lactuca canadensis</i> L.	2.8		
<i>Prenanthes</i> sp.	47.2		
<i>Senecio obovatus</i> Muhl.	2.8		
<i>Senecio pauperculus</i> Michx.	2.8		
<i>Solidago caesia</i> L.	52.8		
<i>Solidago flexicaulis</i> L.	52.8		
<i>Solidago hispida</i> Muhl.	2.8		

Appendix 2. Continued

Taxon	Herbaceous Layer	Shrub Layer	Canopy and Subcanopy
<i>Solidago rugosa</i> P. Mill.	30.6		
<i>Taraxacum officinale</i> Weber ex Wiggers	16.7		
BALSAMINACEAE			
<i>Impatiens capensis</i> Meerb. or <i>I. pallida</i> Nutt.	44.4		
BERBERIDACEAE			
<i>Berberis thunbergii</i> DC.	11.1	11.1	
<i>Caulophyllum thalictroides</i> (L.) Michx.	100.0		
BETULACEAE			
<i>Betula alleghaniensis</i> Britton	44.4	27.8	47.2
<i>Betula lenta</i> L.	22.2	13.9	33.3
<i>Betula papyrifera</i> Marshall	5.6		8.3
<i>Betula populifolia</i> Marshall			2.8
<i>Carpinus caroliniana</i> Walter	5.6	13.9	11.1
<i>Corylus americana</i> Walter	2.8		
<i>Corylus cornuta</i> Marshall	2.8		
<i>Ostrya virginiana</i> (P. Mill.) K. Koch	63.9	69.4	88.9
BRASSICACEAE			
<i>Arabis canadensis</i> L.	2.8		
<i>Cardamine concatenata</i> (Michx.) O. Schwarz	8.3		
<i>Cardamine diphylla</i> (Michx.) A. Wood	50.0		
<i>Cardamine</i> × <i>maxima</i> A. Wood	25.0		
<i>Cardamine pennsylvanica</i> Muhl.	2.8		
CAPRIFOLIACEAE			
<i>Lonicera canadensis</i> Marshall	2.8		
<i>Lonicera tatarica</i> L.	2.8	5.6	
<i>Sambucus racemosa</i> L.	69.4	22.2	
<i>Viburnum acerifolium</i> L.	27.8	2.8	
<i>Viburnum alnifolium</i> Marshall	2.8	2.8	
CORNACEAE			
<i>Cornus alternifolia</i> L. f.	52.8	13.9	2.8
ERICACEAE			
<i>Kalmia latifolia</i> L.	2.8		
FABACEAE			
<i>Amphicarpaea bracteata</i> (L.) Fernald	2.8		
FAGACEAE			
<i>Fagus grandifolia</i> Ehrh.	50.0	72.2	63.9
<i>Quercus rubra</i> L.	36.1		13.9

Appendix 2. Continued

Taxon	Herbaceous Layer	Shrub Layer	Canopy and Subcanopy
FUMARIACEAE			
<i>Dicentra cucullaria</i> (L.) Bernh. or <i>D. canadensis</i> (Goldie) Walp.	75.0		
GERANIACEAE			
<i>Geranium robertianum</i> L.	44.4		
GROSSULARIACEAE			
<i>Ribes cynosbati</i> L.	41.7	11.1	
HAMAMELIDACEAE			
<i>Hamamelis virginiana</i> L.	5.6	11.1	
HYDROPHYLLACEAE			
<i>Hydrophyllum virginianum</i> L.	33.3		
JUGLANDACEAE			
<i>Carya cordiformis</i> (Wangenh.) K. Koch	72.2	11.1	36.1
<i>Carya ovata</i> (P. Mill.) K. Koch	2.8		2.8
<i>Juglans cinerea</i> L.			5.6
LAMIACEAE			
<i>Prunella vulgaris</i> L.	5.6		
<i>Scutellaria lateriflora</i> L.	2.8		
LAURACEAE			
<i>Lindera benzoin</i> (L.) Blume	11.1	5.6	
OLEACEAE			
<i>Fraxinus americana</i> L.	80.6	38.9	72.2
ONOGRACEAE			
<i>Circaea alpina</i> L.	2.8		
<i>Circaea lutetiana</i> L.	66.7		
OXALIDACEAE			
<i>Oxalis stricta</i> L.	2.8		
PAPAVERACEAE			
<i>Chelidonium majus</i> L.	2.8		
<i>Sanguinaria canadensis</i> L.	19.4		
POLYGONACEAE			
<i>Polygonum cilinode</i> Michx.	30.6		
PORTULACACEAE			
<i>Claytonia caroliniana</i> Michx.	63.9		
PRIMULACEAE			
<i>Trientalis borealis</i> Raf.	5.6		

Appendix 2. Continued

Taxon	Herbaceous Layer	Shrub Layer	Canopy and Subcanopy
RANUNCULACEAE			
<i>Actaea rubra</i> (Aiton) Willd. or <i>A. alba</i> (L.) P. Mill.	88.9		
<i>Hepatica acutiloba</i> DC.	16.7		
<i>Hepatica americana</i> (DC.) Ker Gawl.	8.3		
<i>Ranunculus abortivus</i> L.	55.6		
<i>Ranunculus hispidus</i> Michx.	2.8		
<i>Ranunculus recurvatus</i> Poir.	13.9		
<i>Thalictrum dioicum</i> L.	25.0		
RHAMNACEAE			
<i>Rhamnus cathartica</i> L.	2.8		2.8
ROSACEAE			
<i>Fragaria vesca</i> L.	11.1		
<i>Geum canadense</i> Jacq.	30.6		
<i>Prunus serotina</i> Ehrh.	50.0	8.3	16.7
<i>Prunus virginiana</i> L.	22.2	8.3	
<i>Rubus allegheniensis</i> T.C. Porter	50.0	5.6	
<i>Rubus idaeus</i> L.	19.4		
<i>Rubus occidentalis</i> L.	33.3	2.8	
<i>Rubus odoratus</i> L.	47.2	8.3	
<i>Rubus pubescens</i> Raf.	2.8		
RUBIACEAE			
<i>Galium circaezans</i> Michx. or <i>G. lanceolatum</i> Torr.	8.3		
<i>Galium triflorum</i> Michx.	75.0		
<i>Mitchella repens</i> L.	2.8		
SAXIFRAGACEAE			
<i>Mitella diphylla</i> L.	30.6		
<i>Saxifraga virginiana</i> Michx.	22.2		
<i>Tiarella cordifolia</i> L.	66.7		
SCROPHULARIACEAE			
<i>Veronica officinalis</i> L.	2.8		
SOLANACEAE			
<i>Solanum dulcamara</i> L.	16.7		
TILIACEAE			
<i>Tilia americana</i> L.	55.6	38.9	55.6
ULMACEAE			
<i>Ulmus americana</i> L.			13.9
<i>Ulmus rubra</i> Muhl.	41.7	16.7	22.2

Appendix 2. Continued

Taxon	Herbaceous Layer	Shrub Layer	Canopy and Subcanopy
URTICACEAE			
<i>Laportea canadensis</i> (L.) Wedd.	41.7		
<i>Pilea pumila</i> (L.) A. Gray	2.8		
VERBENACEAE			
<i>Phryma leptostachya</i> L.	2.8		
VIOLACEAE			
<i>Viola blanda</i> Willd.	47.2		
<i>Viola canadensis</i> L.	38.9		
<i>Viola pubescens</i> Aiton	52.8		
<i>Viola rostrata</i> Pursh	19.4		
<i>Viola rotundifolia</i> Michx.	30.6		
<i>Viola selkirkii</i> Pursh	2.8		
<i>Viola sororia</i> Willd.	19.4		
VITACEAE			
<i>Parthenocissus quinquefolius</i> (L.) Planch.	30.6		
<i>Vitis</i> sp.	8.3	5.6	
MAGNOLIOPHYTA – LILIOPSIDA			
APIACEAE			
<i>Osmorhiza claytonii</i> (Michx.) C.B. Clarke	61.1		
<i>Sanicula trifoliata</i> E.P. Bicknell	13.9		
ARACEAE			
<i>Arisaema triphyllum</i> (L.) Schott	91.7		
CYPERACEAE			
<i>Carex albursina</i> Sheldon	36.1		
<i>Carex appalachica</i> J.M. Webber & P. Ball	69.4		
<i>Carex arctata</i> W. Boott	13.9		
<i>Carex communis</i> L.H. Bailey	50.0		
<i>Carex debilis</i> Michx.	16.7		
<i>Carex deweyana</i> Schwein.	11.1		
<i>Carex digitata</i> Willd.	5.6		
<i>Carex hitchcockiana</i> Dewey	16.7		
<i>Carex intumescens</i> Rudge	19.4		
<i>Carex laxiculmis</i> Schwein.	5.6		
<i>Carex laxiflora</i> Lam. or <i>C. blanda</i> Dewey or <i>C. leptonevia</i> (Fernald) Fernald	41.7		
<i>Carex pedunculata</i> Muhl.	50.0		
<i>Carex plantaginea</i> Lam.	61.1		
<i>Carex platyphylla</i> Carey	13.9		
<i>Carex rosea</i> Schkuhr or <i>C. radiata</i> (Wahlenb.) Small	16.7		

Appendix 2. Continued

Taxon	Herbaceous Layer	Shrub Layer	Canopy and Subcanopy
<i>Carex sparganioides</i> Muhl.	8.3		
<i>Carex sprengelii</i> Dewey	5.6		
<i>Carex swanii</i> (Fernald) Mackenzie or <i>C. virescens</i> Muhl.	2.8		
LILIACEAE			
<i>Allium tricoccum</i> Aiton	63.9		
<i>Erythronium americanum</i> Ker Gawl.	72.2		
<i>Maianthemum canadense</i> Desf.	36.1		
<i>Medeola virginiana</i> L.	8.3		
<i>Polygonatum pubescens</i> (Willd.) Pursh	83.3		
<i>Smilacina racemosa</i> (L.) Desf.	88.9		
<i>Streptopus roseus</i> Michx.	2.8		
<i>Trillium erectum</i> L.	97.2		
<i>Uvularia sessilifolia</i> L.	38.9		
ORCHIDACEAE			
<i>Epipactis helleborine</i> (L.) Crantz	5.6		
<i>Orchis spectabilis</i> L.	2.8		
POACEAE			
<i>Agrostis</i> sp.	5.6		
<i>Brachyelytrum erectum</i> (Schreber) P. Beauv.	2.8		
<i>Cinna latifolia</i> (Trevir.) Griseb.	8.3		
<i>Elymus hystrix</i> L.	8.3		
<i>Glyceria striata</i> (Lam.) A. Hitchc. or <i>G. melicaria</i> (Michx.) C.E. Hubbard	13.9		
<i>Oryzopsis racemosa</i> (Sm.) Ricker	33.3		
<i>Poa</i> sp.	5.6		
<i>Schizachne purpurascens</i> (Torr.) Swallen	2.8		

APPENDIX 3

List of taxa occurring at $\geq 50\%$ frequency in one or more of the RMF types or subtypes identified by cluster analysis, and indicated by a six-letter taxon abbreviation in the DCA species ordination (Figure 2). Abbreviations consist of the first three letters each of the genus and specific epithet, except in cases where taxa were only identified to genus, for which the first six letters of the genus are used. The species are as follows: *Acer pensylvanicum*, *A. saccharum*, *Actaea* spp., *Adiantum pedatum*, *Allium tricoccum*, *Arisaema triphyllum*, *Asarum canadense*, *Aster divaricatus*, *Athyrium filix-femina*, *A. thelypteroides*, *Betula alleghaniensis*, *Botrychium virginianum*, *Cardamine diphylla*, *Carex albursina*, *C. appalachica*, *C. communis*, *C. hitchcockiana*, *C. laxiflora* s.l., *C. pedunculata*, *C. plantaginea*, *Carya cordiformis*, *Caulophyllum thalictroides*, *Circaea lutetiana*, *Claytonia caroliniana*,

Cornus alternifolia, *Cystopteris fragilis*, *Dicentra* spp., *Dryopteris goldiana*, *D. intermedia*, *D. marginalis*, *Erythronium americanum*, *Eupatorium rugosum*, *Fagus grandifolia*, *Fraxinus americana*, *Galium triflorum*, *Geranium robertianum*, *Geum canadense*, *Hepatica acutiloba*, *Hydrophyllum virginianum*, *Impatiens* spp., *Laportea canadensis*, *Maianthemum canadense*, *Matteuccia struthiopteris*, *Mitella diphylla*, *Oryzopsis racemosa*, *Osmorhiza claytonii*, *Ostrya virginiana*, *Panax trifolius*, *Polygonatum pubescens*, *Polystichum acrostichoides*, *Prenanthes* spp., *Prunus serotina*, *Ranunculus abortivus*, *Ribes cynosbati*, *Rubus allegheniensis*, *R. occidentalis*, *Rubus odoratus*, *Sambucus racemosa*, *Sanguinaria canadensis*, *Saxifraga virginensis*, *Smilacina racemosa*, *Solidago caesia*, *S. flexicaulis*, *Taraxacum officinale*, *Thalictrum dioicum*, *Tiarella cordifolia*, *Tilia americana*, *Trillium erectum*, *Ulmus rubra*, *Uvularia sessilifolia*, *Viola blanda*, *V. canadensis*, *V. pubescens*, *V. rotundifolia*.