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Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests

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Abstract

Aim and location The research investigated the long-term effects of human disturbance, namely nineteenth century agricultural land-use, on the modern species composition, structure and distribution of Rich Mesic Forests (RMF) in western Massachusetts, USA. RMF are a species-rich north-eastern variant of the Mixed Mesophytic Forest Type of eastern North America.

Methods Land-use history patterns were reconstructed for two towns (*c.* 16,000 ha) from the onset of widespread European settlement and agricultural land-use in the late eighteenth century until present. Vegetation and a range of environmental variables were sampled in sixty-one 10×10 m plots in thirty-four forest stands with varying histories of human disturbance. Vegetation data were ordinated (DCA) to identify patterns of variation and related environmental and historical factors. The distribution patterns of individual taxa in relation to historical land-use and environmental factors were analysed using *G*-tests of independence and logistic regression. Associations between species secondary forest colonization ability and life history characteristics (e.g. diaspore dispersal mode, degree of vegetative spread) were assessed.

Results Persistent compositional differences were documented between the vegetation of primary forests and post-agricultural, secondary forests indicating that distribution patterns for many plant species still reflect the open, agricultural environment of the nineteenth century, despite the current predominance of forest cover in the study area. A major factor driving modern vegetation patterns in RMF is the ability and rate of colonization by forest herbs. In particular, species with seeds lacking morphological adaptations for dispersal (barochores) and those which produce seeds with elaiosomes to encourage ant dispersal (myrmecochores) are less frequent in secondary forests. Environmental differences between primary and secondary forests, although present, appear to be less important in influencing species distribution patterns.

Main conclusions Widespread agricultural land-use represents a novel disturbance in the naturally forested ecosystems of eastern North America with long-term impacts on plant community composition and structure. Many secondary forest sites that are environmentally suitable for RMF vegetation do not support the suite of plant species typical of this community type, apparently because of the dispersal limitations of certain forest herbs. These poorly dispersed herb taxa are well adapted for growth in stable forest ecosystems characterized by local, small-scale disturbance (e.g. gap-phase dynamics), yet are maladapted for rapid population recovery and recolonization following severe disturbance (e.g. agricultural land-use).

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Forest herbs, land-use, seed dispersal, relict populations, Rich Mesic Forest, Mixed Mesophytic Forest, disturbance.

INTRODUCTION

Human land-use in the forested ecosystems of eastern North America represents a novel disturbance, unprecedented in its extent, intensity and duration (Matlack, 1994; Foster *et al.*, 1998). Species adapted to forest ecosystems typified by local, small-scale disturbance and gradual change may be unable to persist in landscapes where human land-use intensifies disturbance regimes and results in the reduction or severe modification of forest vegetation (Matlack, 1994). Several authors have suggested that organisms with limited dispersal ability and low reproductive rates may be particularly vulnerable to intense disturbance and habitat fragmentation (Noss & Csuti, 1994; Meier *et al.*, 1995; Hermy *et al.*, 1999). In the north-eastern United States, nutrient-rich, mesophytic forest, commonly termed 'Rich Mesic Forest' (RMF), is a community type that is characterized by numerous forest herb taxa that are thought to have limited seed production and dispersal ability (Matlack, 1994; Meier *et al.*, 1995; McLachlan & Bazely, 2001; Singleton *et al.*, 2001). Despite several centuries of widespread human activity in the region resulting in the predominance of secondary forests growing on post-agricultural land (Foster *et al.*, 1998), little is known of the long-term effects of this disturbance history on the structure, distribution and species composition of RMF. This study coupled historical and cartographical records with field sampling to assess the impacts of historical land-use on modern RMF vegetation.

Rich Mesic Forests are a north-eastern variant of the Mixed Mesophytic Forests of eastern North America (Braun, 1950), a forest type that exhibits broad compositional similarities at the family and generic level with other temperate mesophytic forests in Europe and Asia (Cain, 1943; Braun, 1950). RMF are characterized by *Acer saccharum* Marshall-dominated canopies and a species-rich herb layer, including spring ephemerals such as *Allium tricoccum* Aiton, *Claytonia caroliniana* Michx and *Dicentra canadensis* (Goldie) Walp., as well as summer-green herbs and ferns, including *Asarum canadense* L., *Adiantum pedatum* L. and *Caulophyllum thalictroides* (L.) Michx. (Weatherbee, 1996; Bellemare *et al.*, in preparation). Forest herbs typical of temperate mesophytic forests are often characterized by low annual seed production, a long pre-reproductive growth phase and lack of persistent soil seed banks (Bierzychudek, 1982; Brown & Warr, 1992; Thompson *et al.*, 1998). Numerous taxa produce seeds with elaiosomes that encourage ant dispersal (myrmecochory), or have no morphological adaptations for seed dispersal (barochores; Handel *et al.*, 1981; Grime *et al.*, 1988; Matlack, 1994). These life-history characteristics are believed to represent common adaptations to stable, late successional forest environments (Bierzychudek, 1982). In the north-east, RMF are best developed in western New England and adjacent New York State where their distribution largely coincides with mesic soils on easterly slopes over calcareous bedrock (Weatherbee, 1996; Parnall 1998). The community's limited geographical extent, high species richness and associated rare plant taxa make RMF a conservation priority throughout the region (J.C. Jenkins, 1994, unpublished manuscript; Swain & Kearsley, 2000; MacDougal 2001).

Prior investigations of historical land-use effects in mesophytic forests in the eastern United States and Europe have documented persistent reductions in forest herb species richness following human disturbance (e.g. Peterken, 1974; Peterken & Game, 1984; Dzwonko & Loster, 1988; Matlack, 1994; Singleton *et al.*, 2001). However, most studies have focused on forest stands in fragmented, agricultural landscapes where fields, development or other non-forested habitat may present substantial barriers to colonization of secondary stands (Gerhardt & Foster, 2002). In addition, the long and intensive history of forest use in Europe suggests that even the vegetation of 'primary' stands may be heavily modified by centuries of coppicing, grazing and other human activity. The area investigated in this study presents an opportunity to quantify forest herb recovery patterns in a region that has a relatively short, well-documented history of intensive land-use and is largely forested today.

The objectives of this study were: (1) To assess the effects of past human land-use and environmental variation on the species composition of RMF and the distribution and abundance of individual taxa; (2) To assess the relationships between plant life-history characteristics, patterns of historical land-use and modern species distribution patterns; and (3) To evaluate patterns of forest herb species population recovery at a landscape scale.

Study area

The study area comprised the towns of Conway and Shelburne in western Massachusetts, which include 15,859 ha in the north-eastern foothills of the Berkshire Plateau (Fig. 1). The area is underlain by bedrock of Paleozoic age, principally the Waits River Formation consisting of garnetiferous quartz mica schist with interbeds of impure, calcitic marble (Segerstrom, 1956; Willard, 1956). Physiographically the area is a dissected upland covered to varying depths by glacial till (Segerstrom, 1956). Elevations range from ~50 to 486 m a.s.l. Regional forest vegetation is classified as Transition Hardwoods – White Pine – Hemlock, although our study sites were *A. saccharum*-dominated (Westveld, 1956). The climate is continental, with a mean January temperature of −5.1 °C and mean July temperature of 21.1 °C; precipitation

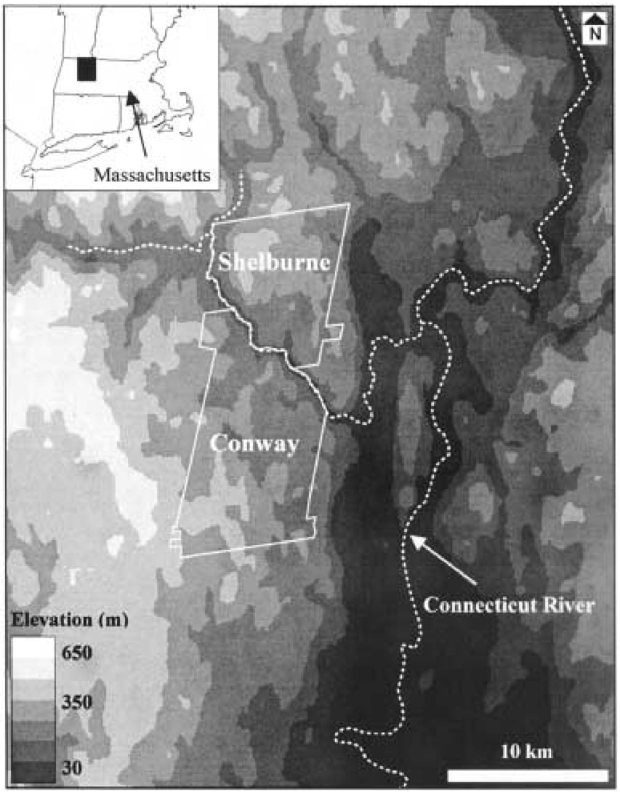

Figure 1 Study area in the towns of Conway and Shelburne on the eastern edge of the Berkshire Plateau in western Massachusetts, USA.

is evenly distributed throughout the year with a mean annual total of 119 cm (Mott & Fuller, 1967).

History of settlement and land cover

There is no archaeological evidence of significant human habitation or impact in the study area prior to the arrival of Europeans in the eighteenth century, although Native Americans undoubtedly used the area seasonally for resource gathering (Anonymous, 1982a,b). At the time of European settlement, the area was predominantly forested; early settlers described a 'rough uncultivated wilderness… covered with thick and heavy woods' (Emerson, 1804 in Lee, 1967). Settlement proceeded rapidly following cessation of the French and Indian Wars, *c*. 1763, with the population exceeding 3000 by 1790 (Fig. 2; Sheldon, 1895; Anonymous, 1982a,b). As in much of the North-east, settlement initiated a period of rapid deforestation; nearly 80% of the landscape was cleared from the early nineteenth century (Figs 2 and 3; Foster *et al*., 1998) through the late nineteenth century. Agricultural land-use during this period was predominantly upland pasture for sheep and other livestock; arable and improved mowing lands comprised only 13–18% of land cover (Tax Records, 1801, 1865, 1875). Significant population losses in the late nineteenth century coincided with a sharp decline in open land after 1900 as many farms were

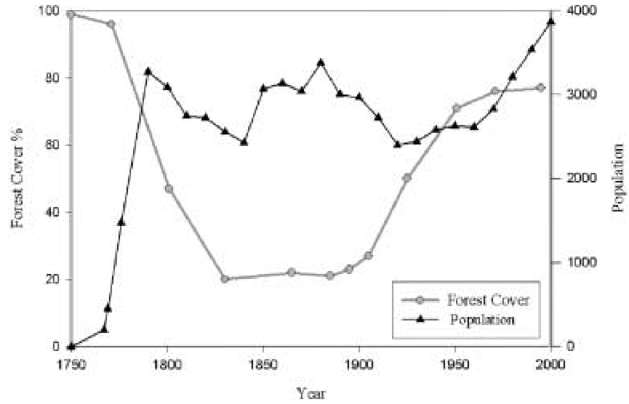

Figure 2 Changes in forest cover and human population in the study area, from 1750 to present. Prior to European settlement in the 1760s, there was no significant year-round human habitation in the area and the landscape was nearly completely forested. Forest cover data are from: Tax Records (1771, 1801, 1865, 1885, 1895, 1905); MA Archives (1830); 1925 (Parmenter, 1928); 1951 and 1971 (MacConnell, 1975); and 1995–97 (Massachusetts Geographic Information System, 2001). Population data for 1767 and 1769 are estimates from Pease (1917); all other data are from the US Federal Census.

abandoned. Forest cover more than doubled between 1885 (21%) and 1925 (50%). By 1952, forest cover exceeded 70% and has remained at comparable levels through the late twentieth century.

MATERIALS AND METHODS

Historical sources documenting past land-use

The earliest maps of forest cover in the study area date from 1830 (MA Archives, 1830). Land cover information from these maps was georeferenced to USGS topographic maps using a zoom transfer scope, and then digitized to create an Arcview GIS coverage. Forest cover in the early twentieth century was derived from 1942 aerial photographs; land cover for this period was classified as: (1) mature forest or (2) open land and early successional forest on abandoned fields. Modern forest cover information (1995–97) was obtained from the MassGIS land-use classification (Massachusetts Geographic Information System, 2001). Using this series of maps, modern forests in the study area were classified as primary (i.e. forested in 1830 and in 1942); nineteenth century secondary (i.e. open land in 1830, but forested by 1942); or twentieth century secondary (i.e. forest on land open or in early successional vegetation in 1942). Following Peterken (1996), 'primary' forest sites have been continuously wooded through the historical period, but are most likely not 'old-growth', as most or nearly all have been managed for the production of maple sugar or as woodlots. 'Secondary' forests have developed on land that was cleared for agricultural use in the past; predominantly pasture for sheep and dairy cows.

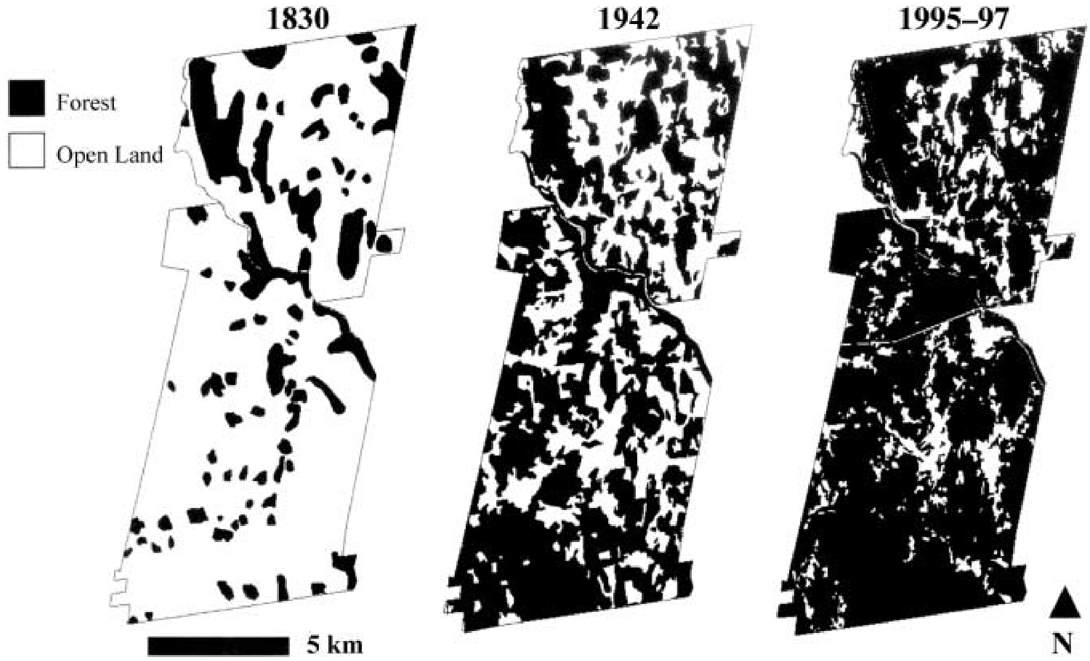

Figure 3 Land cover changes in the study area 1830–1997. Forest extent in 1830 is derived from contemporary land-use maps (MA Archives, 1830). Forest extent in 1942 is derived from aerial photographs; open land was considered to be active fields or recently abandoned fields with early successional forest. Forest cover in 1995–97 was derived from Massachusetts Geographic Information System, (2001).

Table 1 Herbaceous indicator species of Rich Mesic Forests in western Massachusetts. Adapted from Weatherbee (1996), Swain & Kearsley (2000) and field observations of the lead author

Taxa	Common name
Actaea alba (L.) Miller	Doll's eyes
Actaea rubra (Aiton) Willd.	Red baneberry
Adiantum pedatum	Maidenhair fern
Allium tricoccum	Wild leek
Asarum canadense	Wild ginger
Athyrium pycnocarpon (Sprengel) Tidestrom	Glade fern
Cardamine concatenata (Michx.) O. Schwarz	Five-parted toothwort
Cardamine diphylla (Michx.) A. Wood	Broad-leaved toothwort
Cardamine × *maxima* A. Wood	Three-leaved toothwort
Carex plantaginea Lam.	Plantain-leaved sedge
Caulophyllum thalictroides	Blue cohosh
Dicentra cucullaria (L.) Bernh.	Dutchman's breeches
Dicentra canadensis	Squirrel corn
Dryopteris goldiana (Hook.) A. Gray	Goldie's fern
Hepatica acutiloba DC.	Sharp-lobed hepatica
Hydrophyllum virginianum L.	Eastern waterleaf
Osmorhiza claytonii (Michx.) C. B. Clarke	Bland sweet cicely
Sanguinaria canadensis L.	Bloodroot
Thalictrum dioicum L.	Early meadow rue

Modern vegetation and soils

To evaluate the relative influence of current environmental conditions and site history on forest communities, vegetation and soils were sampled in stands with varying histories selected using the following criteria: (i) occurrence on easterly slopes, (ii) *A. saccharum* dominant or co-dominant in the canopy or subcanopy, (iii) the presence of one or more RMF indicator species (Table 1). One to six 10×10-m plots were randomly established in each stand dependent on areal extent and site heterogeneity. The plots were assigned to one of the three past land-use categories based on the historical maps and field evidence of land-use boundaries (e.g. stonewalls). A total of sixty-one plots were established in thirty-four stands: eighteen plots were classified as primary forest, thirty-two as nineteenth century secondary forest and eleven as twentieth century secondary forest.

In each plot, live and dead trees ≥ 2.5 cm diameter at breast height (d.b.h.) were tallied for species, canopy position and d.b.h. Percentage cover was estimated for shrub and herb layer species using a modified version of the Braun–Blanquet scale: 0–1%, 1–12%, 12–50%, 50–75% and > 75%. Nomenclature follows Gleason & Cronquist (1991). Cover of exposed bedrock, rocks and coarse woody debris (CWD) was estimated, and aspect and slope were measured. The presence of seeps and streams, and a qualitative estimate of soil moisture class, was noted. Terrain shape index (TSI) values were calculated by measuring mean slope in eight directions (N, NE, E, SE, S, SW, W, and NW) (McNab, 1989). Solar insolation for May was calculated for each plot using a model incorporating slope, aspect, elevation, longitude and latitude (Ollinger *et al*., 1995). Distance to the nearest bedrock outcrop was estimated in 5-m intervals up to 50 m.

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

Data analysis

Herb layer data were ordinated to identify patterns of vegetation variation and associated environmental gradients using detrended correspondence analysis (DCA) in PCORD (version 4, MjM Software Design, Gleneden Beach, OR, USA) using the Sorensen (Bray–Curtis) metric. A joint plot was used to relate environmental and historical variables to the unconstrained vegetation ordination, with past land-use included as an ordinal variable (primary = 1, nineteenth century secondary = 2, twentieth century secondary = 3). Kruskal–Wallis tests in SYSTAT (version 9, SPSS Inc., Chicago, IL, USA) were used to evaluate differences in environmental variables, canopy and subcanopy basal area and herb layer species richness between primary and secondary forest. *G*-tests of independence (Sokal & Rohlf, 1995) were used to evaluate differences in species frequency among primary and secondary forest. Several species were combined into taxa 'groups' for these analyses, including *Actaea alba* and *A. rubra*, *D. canadensis* and *D. cucullaria*, and *Impatiens capensis* Meerb. and *I. pallida* Nutt. The sedge species *Carex leptonervia* (Fern.) Fern., *C. blanda* Dewey, and *C. laxiflora* Lam. were also grouped for analysis; as were *C. rosea* Schk. and *C. radiata* (Wahlenb.) Small; and *C. swanii* (Fern.) Mackenzie and *C. virescens* Muhl.

Pearson correlations (SYSTAT) were calculated among environmental factors after variables with skewed distributions were transformed to their natural logarithms. Bonferroni adjustments for multiple tests (Rice, 1989) were used to adjust for multiple comparisons in Pearson correlations. Bonferroni adjustments were not calculated for *G*-test and Kruskal–Wallis analyses. Because many significance tests have been performed, some significant results may be spurious; however, most conclusions should be accurate.

To investigate the responses of individual herb layer species to environmental gradients and historical land-use, an exploratory multiple logistic regression (SYSTAT) was used to model species occurrence as a function of six factors: soil C : N ratio, pH, moisture class, silt content, aspect and past land-use. These factors were chosen based on their documented importance to many plant species and the lack of significant correlations between the variables as determined by Pearson correlations. The two qualitative variables were coded as ranked variables for analysis; moisture class: very moist = 3, moist = 2, semimoist = 1; land-use: primary forest = 1, nineteenth century secondary = 2, twentieth century secondary = 3. The distributions of sixty-three taxa occurring in 14–90% of plots were modelled.

Information on selected life-history traits of common herbaceous species (≥ 20% frequency overall) was compiled to assess the relationship between species autecological characteristics and secondary forest colonization ability. To evaluate the association between diaspore dispersal mode and secondary forest colonization ability, a colonization ability index value was calculated for each species as: (frequency in all secondary forest)/(frequency in primary forest). Differences in colonization ability among the four predominant dispersal types, anemochores (wind dispersed seed), barochores, endochores (fruits consumed and dispersed by vertebrates) and myrmecochores, were analysed with Kruskal–Wallis tests. Designations of species diaspore dispersal mode were based on seed morphology and follow those of previous researchers where possible (e.g. Handel, 1976; Montgomery, 1977; Beattie & Culver, 1981; Thompson, 1981; Matlack, 1994; Cain *et al*., 1998; Singleton *et al*., 2001). In several cases dispersal mode of a species was based upon congener designations [e.g. *Claytonia virginica* L. = *C. caroliniana*, *Polygonatum biflorum* (Walter) Elliott. = *P. pubescens* (Willd.) Pursh]. All fern species were classified as wind-dispersed. In addition, species were classified by degree of vegetative spread (clonal, limited clonal growth, not clonal) using information on plant growth form derived from several sources (Gleason, 1952; Gleason & Cronquist, 1991; Matlack, 1994; Cullina, 2000; Singleton *et al*., 2001).

RESULTS

Vegetation characteristics

Acer saccharum comprised 61% of the total basal area in primary stands and occurred in all plots (Table 2). *Carya* *cordiformis* occurred in the canopy of 22% of primary plots, whereas other canopy species were infrequent. *Acer saccharum* dominated the subcanopy and sapling layers of primary stands, along with *Fagus grandifolia* and *Ostrya virginiana*. The herbaceous layer of primary stands was characterized by abundant *C. thalictroides*, *A. tricoccum* and *Polystichum acrostichoides* (Michx.) Schott, each with 4–6% cover. *Acer saccharum* seedlings, *Arisaema triphyllum* (L.) Schott, and *Trillium erectum* L. were frequent (> 75%) at lower abundance. Several taxa showed significantly higher frequency (individual *G*-test $P \leq 0.05$) in primary stands than in secondary, including *A. pedatum*, *Cardamine diphylla*, and *Cardamine* × *maxima* (Table 3). This pattern was particularly strong in the comparison of primary forest and twentieth century secondary forest, where eleven herb and fern species exhibited significantly higher frequency in primary stands.

In nineteenth century secondary forest, *A. saccharum* comprised 81% of the total basal area and was present in 97% of plots. *Carya cordiformis* occurred in 31% of plots and *Betula lenta* occurred in 13% of plots (Table 2). The subcanopy and sapling layer was composed predominantly of *A. saccharum* and *O. virginiana*. The herbaceous layer of nineteenth century secondary stands was dominated by *C. thalictroides*, *Aster divaricatus* and *P. acrostichoides*; all with cover values of 3–6%. *Acer saccharum* seedlings, *A. triphyllum,* and *P. pubescens*, occurred frequently (> 75%), but with low cover. *Aster divaricatus* and *Sanguinaria canadensis* were significantly more frequent in nineteenth century secondary stands than in primary forest (Table 3), while seedlings of *Fraxinus americana* and *O. virginiana* were more abundant.

Twentieth century secondary forests had a substantial component of *A. saccharum* in the canopy and subcanopy (82% frequency, 32% of total basal area), but also included *Betula lenta*, *B. papyrifera* and *Prunus serotina* at levels significantly higher than in primary forest (Table 2). The subcanopy included a greater component of *O. virginiana* than in primary forest. The high frequency and cover of *Polystichum acrostichoides* and *A. saccharum* seedlings characterized the herbaceous layer. *Arisaema triphyllum*, *Dryopteris marginalis* and *Carex* cf. *swanii* were common

Table 2 Canopy and subcanopy characteristics of historical forest types: species basal area (BA) and percent frequency (%). Only taxa occurring in ≥ 2 plots/strata and exhibiting mean BA ≥ 0.005 $m^2\ ha^{-1}$ are listed. Species with significantly different BA (Kruskal–Wallis test) between primary vs. nineteenth century secondary forest and primary vs. 20th C. secondary forest are indicated in bold

	Primary forest (n = 18)		Nineteenth century secondary (n = 32)		Twentieth century secondary (n = 11)	
	BA ($m^2\ ha^{-1}$)	%	BA ($m^2\ ha^{-1}$)	%	BA ($m^2\ ha^{-1}$)	%
Total BA	23.03	NA	31.68	NA	33.48	NA
Canopy						
Acer saccharum	12.66	78	24.44	91	9.79	64
Betula alleghaniensis Britton	0.53	11	0.62	3	0.00	0
***Betula lenta* L.**	0.00	0	0.79	13	**7.21****	73
***Betula papyrifera* Marshall**	0.00	0	0.00	0	**1.69***	27
Carya cordiformis (Wangenh.) K. Koch	2.05	22	2.30	31	0.52	18
Carya ovata (Miller) K. Koch	0.00	0	0.25	3	1.33	18
Fagus grandifolia Ehrh.	0.80	6	0.00	0	0.13	9
Fraxinus americana L.	1.83	6	0.00	0	1.26	9
Pinus strobus L.	0.00	0	0.00	0	3.95	18
***Prunus serotina* Ehrh.**	0.00	0	0.00	0	**1.40***	27
Tilia americana L.	0.22	6	0.32	3	0.00	0
Subcanopy and saplings ≥ 2.5 cm d.b.h.						
Acer saccharum	1.39	94	1.20	84	0.98	82
Acer spicatum Lam.	0.00	0	0.01	9	0.00	0
Betula alleghaniensis	0.01	6	0.01	3	0.05	9
Betula lenta	0.03	6	0.03	13	0.08	18
Carya cordiformis	0.00	0	0.01	3	0.05	18
Fagus grandifolia	0.16	39	**0.05***	13	0.14	27
Fraxinus americana	0.01	6	0.09	16	0.13	18
Hamamelis virginiana L.	0.01	6	0.07	9	0.13	9
***Ostrya virginiana* (Miller) K. Koch**	0.10	28	0.13	28	**0.60***	64
Tilia americana	0.11	11	0.03	13	0.09	9
Tsuga canadensis L. (Carriere)	0.18	22	0.13	6	0.00	0
Ulmus rubra Muhl.	0.06	6	0.01	3	0.00	0
***Vitis* spp. L.**	0.13	28	**0.04***	6	0.03	9

*= $P \leq 0.05$, **$P \leq 0.01$.

Table 3 Percent frequency (%) and seed morphological dispersal type of RMF ground layer taxa in stands with differing histories. Taxa listed include those for which *G*-tests were possible and three taxa that were too frequent for *G*-test analysis (+). Dispersal types include: anemochore (ANE), ballistichore (BAL), barochore (BAR), endozoochore (END), exozoochore (EXO), myrmecochore (MYR) and vegetative spread only (VEG). *G*-test analyses were run as primary forest vs. nineteenth century secondary and primary forest vs. twentieth century secondary. Significant results are indicated in bold

Taxa	Dispersal	Primary %	Nineteenth century secondary %	Twentieth century secondary %
Cardamine* × *maxima	VEG	50	**3*** **	**0*** **
Cardamine diphylla	BAR	78	**28*** **	**9*** **
Adiantum pedatum	ANE	61	**25* **	**9** **
Carex plantaginea	BAR	50	28	**0*** **
Asarum canadense	MYR	67	38	**0*** **
Trillium erectum	MYR	89	66	**18*** **
***Tiarella cordifolia* L.**	BAR	56	34	**9** **
Claytonia caroliniana	MYR	56	34	**9** **
***Actaea* spp.**	END	56	59	**9** **
***Athyrium thelypterioides* (Michx.) Desv.**	ANE	67	50	**9** **
***Galium triflorum* Michx.**	EXO	50	34	**9* **
Sambucus racemosa L.	END	28	9	0
Osmorhiza claytonii	EXO	28	9	0
Laportea canadensis (L) Wedd.	BAR	28	13	0
Allium tricoccum	BAR	56	28	18
Fagus grandifolia	END	33	16	18
Rubus odoratus L.	END	28	19	0
Carex appalachica J. M. Webber & P. Ball	BAR	28	13	18
Dryopteris goldiana	ANE	22	16	0
Lindera benzoin (L) Blume	END	28	19	9
Erythronium americanum Ker Gawler	MYR	56	38	18
Geranium robertianum L.	BAL	22	19	0
Solidago flexicaulis L.	ANE	33	28	0
Acer pensylvanicum L.	ANE	22	6	36
Circaea lutetiana L.	EXO	44	34	18
Onoclea sensibilis L.	ANE	22	19	9
Caulophyllum thalictroides	END	83	66	55
Acer saccharum (+)	ANE	83	97	91
Polystichum acrostichoides (+)	ANE	89	94	100
Arisaema triphyllum (+)	END	94	81	82
Carex albursina Sheldon	BAR	28	19	27
Impatiens spp.	BAL	33	31	9
Carex laxiflora s.l.	BAR	33	25	27
Dicentra spp.	MYR	39	44	0
Osmunda claytoniana L.	ANE	22	16	27
Dryopteris intermedia (Muhl.) A. Gray	ANE	61	56	36
Rubus allegheniensis T. C. Porter	END	33	25	36
Smilacina racemosa (L) Desf.	END	56	53	36
Solidago rugosa Miller	ANE	17	19	9
Parthenocissus quinquefolia (L) Planchon	END	17	16	18
Polygonatum pubescens	END	67	78	36
Athyrium filix-femina (L) Roth	ANE	50	59	27
Maianthemum canadense Desf.	END	22	19	36
Ribes cynosbati L.	END	17	19	18
Carex pedunculata Muhl.	MYR	17	25	0
Viola pubescens Aiton.	MYR	11	19	0
Solidago caesia L.	ANE	33	47	27
Tilia americana	ANE	22	31	27
Rubus occidentalis L.	END	17	19	36
Dryopteris marginalis (L) A. Gray	ANE	39	66	55
Hepatica acutiloba	MYR	11	25	0
Cornus alternifolia L.f.	END	11	22	27
Berberis thunbergii DC.	END	11	19	36
Viburnum acerifolium L.	END	11	19	45

Table 3 *continued*

Taxa	Dispersal	Primary %	Nineteenth century secondary %	Twentieth century secondary %
Viola rostrata Pursh.	MYR	6	25	18
Carex rosea s.l.	BAR	6	25	18
Aster cf. lanceolatus Willd.	ANE	6	22	36
Carya cordiformis	END	39	44	**82***
Betula cf. lenta	ANE	11	22	**55***
Sanguinaria canadensis	MYR	6	**28***	27
***Aster divaricatus* L.**	ANE	50	**88****	45
Prunus serotina	END	22	34	**82****
Fraxinus americana	ANE	28	56	**100*****

*$P \leq 0.05$, **$P \leq 0.01$, and ***$P \leq 0.001$.

(> 50% frequency), but exhibited low cover. Seedlings of *F. americana*, *P. serotina*, *B. lenta* and *C. cordiformis* were significantly more frequent in twentieth century secondary forest than in primary forest (Table 3).

Richness of herbaceous and woody species in the herb layer did not differ significantly among primary and nineteenth century secondary stands. Primary forest had a median of twenty-three herbaceous taxa/plot and nineteenth century secondary a median of twenty herbaceous taxa/plot ($P = 0.107$). Primary forest had a median of five woody taxa/plot and nineteenth century secondary a median of seven taxa/plot ($P = 0.179$). In contrast, primary forest had significantly higher herbaceous species richness than twentieth century secondary stands (twenty-three taxa/plot vs. thirteen taxa/plot, $P = 0.001$), and woody species richness was significantly lower in the herb layer of primary forest (five taxa/plot vs. eleven taxa/plot, $P < 0.001$).

Ordination of vegetation data suggested similar patterns to those indicated by comparisons of species richness; primary and nineteenth century secondary forest plots overlapped substantially along DCA Axis 1, but twentieth century secondary forest plots had high Axis 1 scores and were distinct from primary forest (Fig. 4a). Primary and nineteenth century secondary forest vegetation were not clearly separated along DCA Axis 2, while eight of eleven plots in twentieth century secondary forest had high Axis 2 scores. 'After-the-fact' coefficients of determination (McCune & Mefford, 1999) indicated that Axis 1 accounts for most of the variance explained (Axis 1, $r^2 = 0.405$; Axis 2, $r^2 = 0.059$).

Environmental characteristics

Several environmental variables were significantly correlated ($P \leq 0.05$; see Appendix 1). Soil C and N percentage were positively correlated with TEC, SOM%, and cation concentrations (e.g. Ca and Mg ppm) and negatively correlated with bulk density. Soil pH was positively correlated with Ca and Mg concentrations and negatively correlated with iron (Fe) and aluminium (Al) concentrations. Presence and depth of the O layer was negatively correlated with A horizon depth. Proximity to bedrock outcrops was positively correlated with soil N% and C%, TEC and SOM%. Historical land-use was not significantly correlated with any environmental variable. Few significant differences in environmental characteristics were detected between primary and nineteenth century secondary stands (Table 4). Greater environmental variation was detected between primary and twentieth century secondary forest. Ca and Mg concentrations were significantly lower in twentieth century secondary forest, and Al concentrations were higher.

Joint plot analysis of DCA output (Fig. 4a) indicated land-use as the predominant factor associated with vegetation variation along Axis 1 of the ordination ($R = 0.67$), followed by B concentration ($R = -0.48$) and soil clay content ($R = 0.45$). Axis 2 of the ordination was associated with SMP buffer pH ($R = -0.48$) and moisture class ($R = -0.44$).

Physiography and land-use

In order to further explore factors influencing vegetation variation among primary and nineteenth century secondary stands, an additional ordination was conducted excluding twentieth century secondary stands. For this set of plots ($n = 50$), DCA ordination indicated an interesting pattern relative to distance from bedrock outcrops. Whereas plots in nineteenth century secondary forest stands < 50 m from bedrock and those in primary forest (both < and > 50 m from bedrock) had low Axis 1 scores, nineteenth century secondary plots > 50 m from bedrock had high Axis 1 scores and were distinctly separated along Axis 1 (Fig. 5). *G*-test analysis of species frequency in primary and nineteenth century secondary plots < 50 m and > 50 m from bedrock indicated similar patterns; few differences were detected between primary forest and nineteenth century secondary plots < 50 m from bedrock outcrops, but for plots > 50 m from outcrops, several species exhibited significant differences (Table 5). These included *Asarum canadense*, *C. thalictroides* and *C. diphylla*, which were more frequent in primary forest plots > 50 m from outcrops (*G*-test $P < 0.01$), and *F. americana* seedlings which were more frequent in nineteenth century secondary plots > 50 m from bedrock (*G*-test $P = 0.005$). Primary forest plots > 50 m bedrock had significantly higher richness of herbaceous species than nineteenth century secondary plots > 50 m

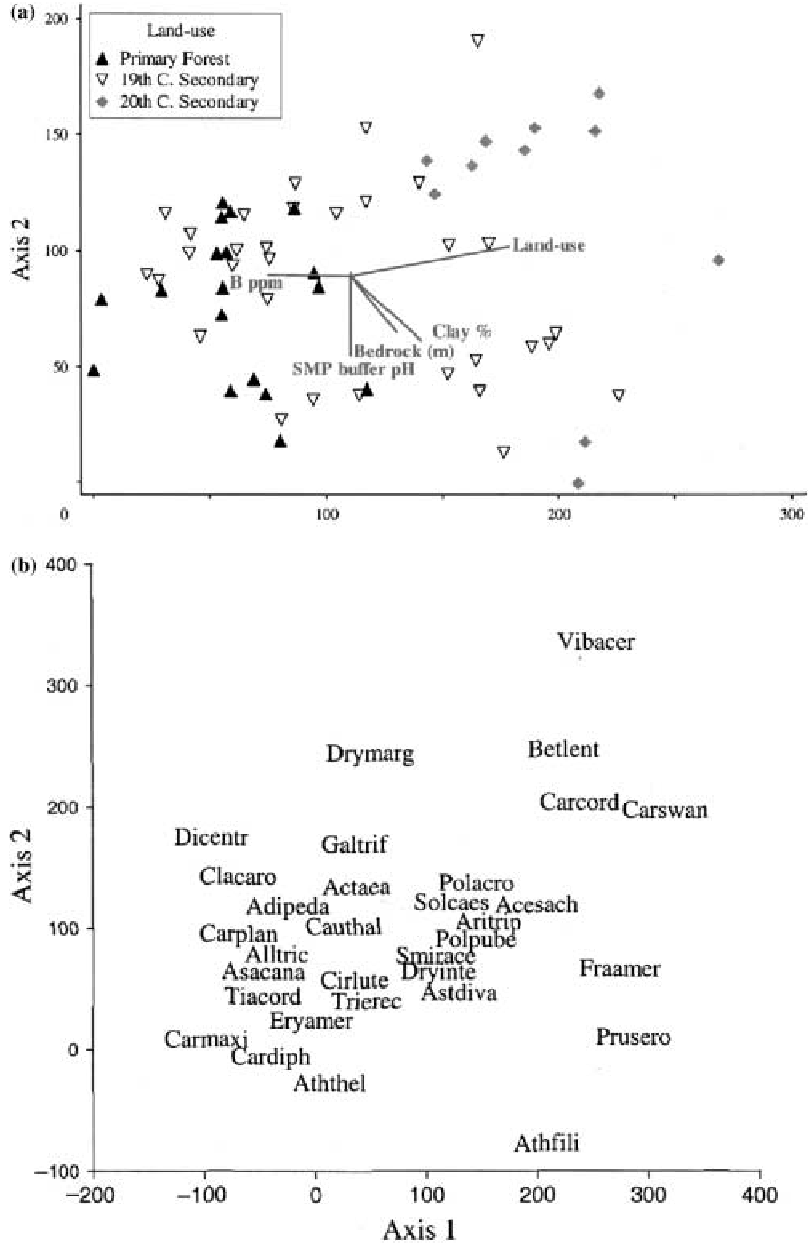

Figure 4 DCA ordination of sixty-one vegetation plots (a) with historical class indicated, and joint plot of environmental factors related to major axes of variation ($r^2 \geq 0.200$). DCA ordination of common herb layer species (b); only taxa occurring in $\geq 40\%$ of plots in one or more of the historical classes are labelled. Species abbreviations are the first three letters of genus and first four letters of species. For taxa only identified to genus, the first seven letters of the genus are used. Taxa represented are listed in Appendix 2.

(median of twenty-two taxa/plot vs. sixteen taxa/plot, $P = 0.032$). Woody species richness was significantly lower in the ground layer of primary plots > 50 m bedrock (five taxa/plot vs. seven taxa/plot, $P = 0.044$). Environmental conditions in primary and nineteenth century secondary plots > 50 m from bedrock were comparable (data not shown), only Fe and B concentrations differed significantly ($P = 0.022$ and $P = 0.043$), being higher in primary stands.

Predictors of individual species distributions

The distributions of approximately two-thirds of the sixty-three herb layer taxa analysed were significantly correlated with one or more of the six environmental and historical variables included in the regression model (Table 6). The distributions of twenty-three taxa were significantly correlated with past land-use, fifteen taxa were correlated with soil C : N ratio, and eight taxa were correlated with aspect. Other variables had fewer significant correlations. Land-use was the only or strongest significant predictor for sixteen taxa.

Life-history characteristics and land-use history

In the analysis of secondary forest colonization ability, significant differences (Kruskal–Wallis test $P = 0.042$) were identified among the four predominant diaspore dispersal types represented among herbaceous species present in $\geq 20\%$ of plots: anemochores ($n = 9$),

Table 4 Environmental characteristics of historical forest types. Values presented are medians with significant differences (Kruskal–Wallis test) between primary vs. nineteenth century secondary, and primary vs. twentieth century secondary forest indicated in bold

	Primary (n = 18)	Nineteenth century secondary (n = 32)	Twentieth century secondary (n = 11)
Physiographic characteristics			
Bedrock cover percentage	0	**0*(+)**	0
Aspect°	68	86	**96****
CWD cover (%)	4	4	**5***
Rock cover (%)	2	2	1
TSI	1.08	0.73	−0.67
Insolation (MJ m^2 day^{-1})	20.28	20.99	21.05
Slope°	21.5	18.5	17.0
Distance to bedrock (m)	≥ 50	10–15	≥ 50
Soil morphology and physical characteristics			
O layer (cm)	0.0	0.3	0.0
A horizon (cm)	18	16	17
Bulk density (g cm^{-3})	0.68	0.61	0.62
Clay percentage	2.92	2.92	2.92
Silt percentage	27.6	29.6	29.1
Sand percentage	69.5	67.5	66.0
SOM percentage	8.5	9.9	8.9
Soil minerotrophic status			
B ppm	0.66	**0.46***	**0.44****
Al ppm	964	**1185***	**1343****
Ca ppm	1548	949	**823***
Mg ppm	72	58	**55***
Soluble sulphur	29.5	35.5	**36.0***
SMP buffer pH	6.3	6.1	**6.0***
Zn ppm	4.5	4.1	**3.0***
Cu ppm	2.2	1.9	**1.4***
Soil N%	0.35	0.40	0.33
Soil C%	4.72	5.05	4.75
Soil pH	5.4	5.1	4.9
C:N ratio	13.64	13.40	14.24
TEC	16.08	16.74	16.33
Na ppm	20.5	20.5	16.0
Easily extractable P ppm	31.5	28.5	34.0
K ppm	60	57	50
Mn ppm	94	115	98
Fe ppm	162	152	163

CWD, coarse woody debris; TSI, terrain shape index. Significance levels: *$P \leq 0.05$, **$P \leq 0.01$.

barochores ($n = 6$), endochores ($n = 6$) and myrmecochores ($n = 6$). Other dispersal types, such as exozoochores (adhesive seeds) and ballistochores (explosively dispersed seed), were represented by only one or two taxa with ≥ 20% frequency and were not included in the analysis. Pairwise comparisons of dispersal types indicated that anemochores and endochores exhibited greater colonization ability than barochores ($P = 0.034$ and $P = 0.008$, respectively); a similar trend of greater colonization ability by endochores than myrmecochores was present, but not significant ($P = 0.092$), due in part to the influence of *S. canadensis*, a myrmecochore that was more frequent in secondary forest than primary. Other pairwise comparisons of colonization ability (e.g. barochores vs. myrmecochores, endochores vs. anemochores) were not significant.

No significant differences were detected in secondary forest colonization ability among herbaceous species with varying degrees of clonal growth.

DISCUSSION

Although a moderate level of environmental variation exists among sites with differing histories, the results of this study indicate that extensive nineteenth century forest clearance and land-use, resulting in the severe reduction or local extinction of populations of forest plant species, remains an overriding factor influencing modern vegetation composition and structure in RMF. The long-term persistence of these patterns results in large part from the biological characteristics (e.g. diaspores lacking adaptations for long distance dispersal) of certain plant species associated with this vegetation type.

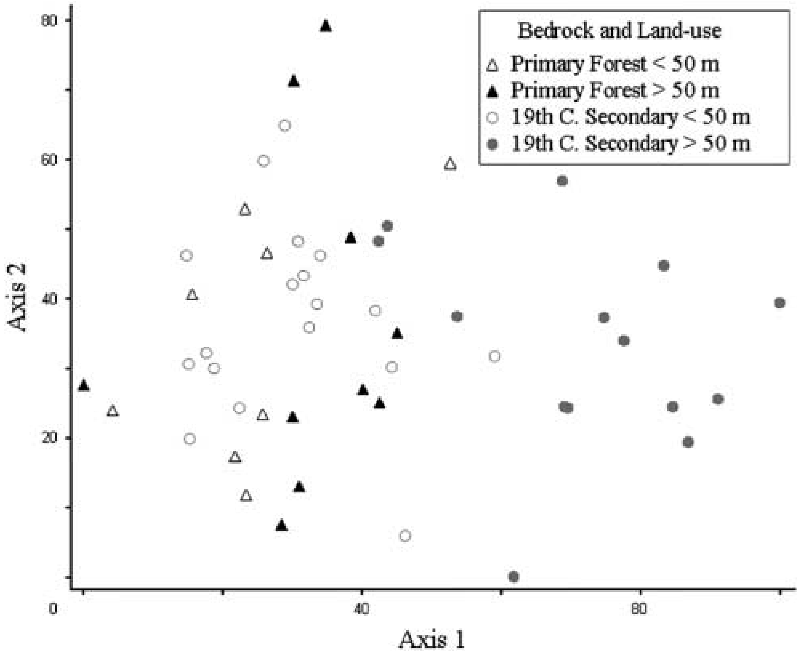

Figure 5 DCA ordination of fifty vegetation plots in primary and nineteenth century secondary forest with plots categorized by bedrock outcrop proximity (> or < 50 m).

Environmental variation among primary and secondary stands

Cation concentrations (Ca, Mg) were highest in primary forest, lowest in twentieth century secondary stands, and intermediate in nineteenth century secondary stands. Whether this variation predates agricultural land-use, or is partly a result of this history, soil Ca and Mg concentrations for secondary forest plots do not differ significantly (Kruskal–Wallis test, $P > 0.10$) from values documented at other sites in western Massachusetts supporting RMF vegetation (Bellemare *et al.*, in preparation), suggesting that the soil nutrient status of secondary forest sites is not limiting for most forest herbs. However, vegetation composition prior to forest clearance and agricultural land-use may have varied in response to this nutrient gradient; in particular, secondary forest sites with lower Ca concentrations may never have been suitable for taxa associated with highly calcareous soils, such as *Athyrium pycnocarpon* and *D. goldiana* (Rawinski, 1992; Bellemare *et al.,* in preparation).

Current differences in nutrient status may also reflect the influence of past land-use and stand age on soil properties. For instance, forest clearance may have resulted in increased leaching of calcium and other cations (Likens *et al*., 1970; Albert & Barnes, 1987; Johnson *et al*., 1997), while overgrazing of pastures and the export of nutrients in farm products may have compounded these losses (Whitney, 1994). These impacts may be greater in areas that were utilized more intensively or for longer periods of time, such as on twentieth century secondary forest sites, which were in use until the early twentieth century and tend to be less rocky and have more moderate slopes than nineteenth century secondary forest sites. In addition, the relatively short period of time since establishment of secondary forests may be inadequate for *A. saccharum* and other 'nutrient-pumping' tree species to increase surface soil cation concentrations through the production of nutrient-rich leaf litter (Youngberg, 1951; Curtis, 1959). The absence of a well-developed herb layer of spring ephemerals in regenerating secondary forest may also limit on-site nutrient retention in comparison to primary forests, where these species are abundant (Muller & Bormann, 1976; Blank *et al*., 1980; Nault & Gagnon, 1988).

The pattern of decreasing frequency from primary to secondary forest of several less nutrient-demanding RMF herbs (e.g. *A. canadense, C. diphylla, Osmorhiza claytonii*) and for herbs typical of relatively nutrient-poor northern hardwoods vegetation (e.g. *C. caroliniana, Erythronium americanum, Tiarella cordifolia*) suggests that past land-use is an important factor controlling distribution patterns of these species (Rawinski, 1992; Thompson & Sorenson, 2000; Bellemare *et al.,* in preparation). This conclusion is strongly supported by regression analysis of individual species distributions, as past land-use emerges as a significant predictor more often than environmental factors related to soil fertility (e.g. pH, C : N ratio). While species undoubtedly respond to these edaphic factors on a broader scale, our results indicate that within the limited range of sites sampled, past land-use is a dominant factor driving vegetation patterns.

The biological legacies of past land-use

Unlike windstorms or selective cutting which typically have a limited impact on ground layer vegetation (Collins & Pickett, 1988; Hughes & Fahey, 1991; Cooper-Ellis *et al*.,

Table 5 Species frequency (%) in the herb layer of primary and nineteenth century secondary forest, with plots categorized by distance to bedrock outcrops. Only taxa occurring in ≥ 50% of plots in at least one category are listed. Significant differences in frequency, determined by *G*-test analyses, are indicated in bold

	Primary ≥ 50 m ($n = 10$)	Nineteenth century ≥ 50 m ($n = 14$)	Primary ≤ 50 m ($n = 8$)	Nineteenth century ≤ 50 m ($n = 18$)
Barochores	%	%	%	%
Allium tricoccum	40	7	75	44
Cardamine diphylla	**80**	**14****	75	39
Cardamine × maxima	50	7	50	0
Carex plantaginea	40	7	63	44
Tiarella cordifolia	**60**	**14***	50	50
Myrmecochores				
Asarum canadense	**70**	**14****	63	56
Claytonia caroliniana	50	0	63	61
Dicentra spp.	30	0	50	78
Erythronium americanum	60	29	50	44
Trillium erectum	80	50	100	78
Endozoochores				
Actaea spp.	30	36	88	78
Arisaema triphyllum	90	100	100	67
Caulophyllum thalictroides	**90**	**36****	75	89
Polygonatum pubescens	70	86	63	72
Smilacina racemosa	40	50	75	56
Anemochores				
Adiantum pedatum	50	14	75	33
Aster divaricatus	60	86	**38***	**89**
Athyrium filix-femina	60	86	38	39
Athyrium thelypterioides	60	43	75	56
Dryopteris intermedia	60	57	63	56
Dryopteris marginalis	20	21	63	100
Polystichum acrostichoides	100	86	75	100
Solidago caesia	20	29	50	61
Exozoochores				
Circaea lutetiana	40	36	50	33
Galium triflorum	60	21	38	44

*$P \leq 0.05$ and **$P \leq 0.01$.

1999), conversion to agriculture may result in the local elimination of all forest species. Populations of forest herbs may be eradicated by soil disturbance and the burning of slash, through exposure and desiccation (Randall, 1953; Meier *et al*., 1995), competition with sod-forming pasture grasses (Kucera, 1952), and intense grazing and trampling (Marks, 1942; Whigham & Chapa, 1999). Following agricultural abandonment, forest herbs must recolonize through seed dispersal from extant populations, as they typically lack extended seed dormancy (Thompson *et al*., 1998; Leckie *et al*. 2000; Baskin & Baskin, 2001) and have limited rates of clonal expansion (Matlack, 1994; Donohue *et al*., 2000).

The variability in secondary forest colonization rates among herb species has been attributed to differing modes of diaspore dispersal (Dzwonko, 1993; Matlack, 1994; Brunet & Von Oheimb, 1998). Our findings corroborate previous studies, in that barochores (e.g. *C. diphylla, T. cordifolia*), and myrmecochores (e.g. *A. canadense, C. caroliniana*) are common in primary forest, but are less frequent or absent in nineteenth and twentieth century secondary stands. *Cardamine × maxima*, a taxon almost entirely restricted to primary forest, represents an extreme example of dispersal limitation, as it is believed to be a sterile hybrid, reproducing exclusively through clonal growth (Gleason & Cronquist, 1991; Cullina, 2000; Fig. 6a). In contrast, endozoochorous and anemochoric taxa that are common in primary forest (e.g. *A. triphyllum*, *C. thalictroides, P. acrostichoides, A. divaricatus*) have colonized many secondary stands, often within a few decades of stand initiation (cf. Dzwonko, 1993; Matlack, 1994). The abundance of the anemochores *A. divaricatus* and *P. acrostichoides* in secondary forests has been noted previously (Glitzenstein *et al*., 1990; Jenkins & Parker, 2000); in this study, *P. acrostichoides* was found to be the most abundant herbaceous species in twentieth century secondary forests, with 100% frequency and mean cover of 5.2%. Despite the success of certain anemochores and endozoochores in colonizing secondary forest, the decreasing frequency of many herbaceous taxa from primary to

Table 6 Exploratory multiple logistic regressions of species occurrence in the ground layer. Sixty-three taxa occurring in 14–90% of the sixty-one plots included in the study were tested; results are presented for the forty-four taxa exhibiting significant correlations ($P \leq 0.05$). Values reported for environmental and historical factors are t-ratios. For land-use, negative values indicate association with primary forest; positive values indicate association with secondary forest. McFadden's ρ^2 indicates the degree to which the model explains species presence or absence

Taxa	%	Land use	C : N	pH	Moisture	Silt percentage	Aspect	ρ^2
Allium tricoccum	34	**−2.70****	−0.49	0.62	−1.37	−0.02	**2.82****	**0.25****
Acer pensylvanicum	16	0.15	0.88	**−2.35***	−1.80	−0.89	−0.93	**0.24***
Actaea spp.	49	**−2.32***	−0.83	0.18	−0.58	0.64	1.37	0.10
Adiantum pedatum	33	**−2.46***	−0.21	0.42	1.29	−0.52	−0.21	**0.17***
Asarum canadense	39	**−2.94****	**−2.41***	**2.32***	0.77	1.51	−0.22	**0.35****
Aster cf. *lanceolatus*	20	**2.47***	0.68	1.10	**2.13***	−0.40	−0.86	**0.26***
Athyrium thelypterioides	48	**−2.57****	0.04	1.72	**3.19****	0.19	1.18	**0.36****
Betula cf. *lenta*	25	**2.95****	−0.24	1.22	−1.34	−1.27	**−2.43***	**0.26****
Caulophyllum thalictroides	69	**−2.44***	1.88	−0.06	−1.24	1.03	1.90	**0.18***
Cardamine diphylla	39	**−3.10****	−0.05	−0.81	−0.33	−1.04	−1.24	**0.25****
Cardamine × *maxima*	16	**−2.38***	−1.54	1.81	0.14	−1.24	−1.56	**0.67****
Carex appalachica	18	−1.47	0.57	−0.15	0.08	0.68	**2.76****	0.20
Carex plantaginea	30	**−2.11***	0.65	0.68	−0.60	−1.72	−0.71	**0.19***
Carex swanii s.l.	15	**2.94****	0.23	−0.52	0.25	1.24	0.21	**0.35****
Carya cordiformis	49	**2.00***	1.13	**−2.50***	−0.40	−0.55	−1.92	**0.21****
Circaea lutetiana	34	−1.06	**−2.77****	1.23	1.60	−0.30	−0.08	**0.20***
Claytonia caroliniana	36	**−2.41***	**−2.32***	−0.50	**−2.31***	−0.62	−0.20	**0.25****
Cornus alternifolia	20	1.72	−0.50	0.71	**1.97***	−0.15	−1.12	0.18
Dicentra spp.	34	**−2.04***	**−2.41***	−0.53	−1.79	−0.01	0.94	**0.20***
Dryopteris goldiana	15	−1.10	**−1.97***	1.49	0.27	0.34	0.72	0.20
Dryopteris intermedia	54	−0.91	−1.53	1.09	1.19	**3.09****	−1.79	**0.31****
Dryopteris marginalis	56	0.08	**−2.60****	**−2.07***	−0.45	−1.18	1.93	**0.21****
Erythronium americanum	39	−1.52	−0.72	1.16	**−2.12***	−0.11	−0.77	0.13
Fagus grandifolia	21	−0.99	**2.01***	−0.48	−0.74	0.23	−1.01	0.11
Fraxinus americana	56	**3.64****	0.94	−0.15	1.75	−1.37	−1.52	**0.31****
Geranium robertianum	16	−1.23	**−2.46***	1.69	0.66	0.56	1.63	**0.30***
Impatiens spp.	28	−1.37	−1.05	0.44	**2.58****	0.17	0.91	**0.22***
Laportea canadensis	15	−1.38	**−2.27***	0.52	1.69	−0.11	−0.32	**0.36****
Maianthemum canadense	23	1.23	1.63	0.40	−1.26	**−2.37***	−1.17	0.19
Onoclea sensibilis	18	0.40	**2.00***	**2.77****	1.53	1.56	−1.04	**0.33****
Ostrya virginiana	16	**2.01***	−0.21	0.85	−1.92	−1.05	−0.14	0.19
Parthenocissus quinquefolia	16	0.73	**−2.46***	0.84	−1.52	−0.35	−0.13	**0.24***
Prunus virginiana	15	**2.66****	1.90	0.41	**2.03***	0.67	−0.19	**0.38****
Prunus serotina	39	**2.87****	**2.07***	−1.17	0.44	−0.06	−1.31	**0.22****
Ranunculus abortivus	15	0.59	**−2.59****	−0.41	−0.30	−1.71	−0.09	**0.32***
Rubus allegheniensis	30	−0.28	0.82	1.34	0.12	0.76	**2.19***	0.12
Rubus occidentalis	21	0.65	1.76	−1.47	1.06	−0.36	**2.58****	**0.23***
Smilacina racemosa	51	−1.37	1.40	−1.75	1.38	**−2.00***	1.51	**0.16***
Solidago caesia	39	−1.10	0.86	−1.65	0.40	−0.94	**2.65****	**0.16***
Solidago flexicaulis	25	**−2.29***	0.27	0.99	1.32	0.35	**3.10****	**0.34****
Taraxacum spp.	18	**2.02***	1.83	0.71	−0.03	−0.33	**2.06***	**0.30****
Tiarella cordifolia	36	**−2.18***	**−2.26***	−0.91	1.39	−1.22	−0.24	**0.21***
Tilia americana	28	1.22	**−2.25***	1.05	−1.57	−1.27	−0.91	0.15
Trillium erectum	64	**−3.42****	1.02	−0.73	0.61	0.03	1.70	**0.25****

$^*P \leq 0.05$, $^{**}P \leq 0.01$.

nineteenth century secondary to twentieth century secondary forests indicates a lengthy colonization gradient that may span centuries for 'slower' taxa (Peterken & Game, 1984; Matlack, 1994; Brunet & Von Oheimb, 1998).

While dispersal mode is apparently associated with colonization patterns for many species, some myrmecochores and barochores do occur frequently in secondary stands (e.g. *Trillium erectum*, *Carex* spp.); conversely, *A. pedatum*, a fern with wind-dispersed spores, is strongly associated with primary forest. The distribution patterns of these species emphasize the need to consider the importance of other autecological characteristics, such as rates of diaspore production or unique establishment requirements. Similarly, the potential for unusual dispersal events, such as vertebrate dispersal of barochores and myrmecochores (e.g. Handel, 1976; Nault & Gagnon, 1993), should not be overlooked.

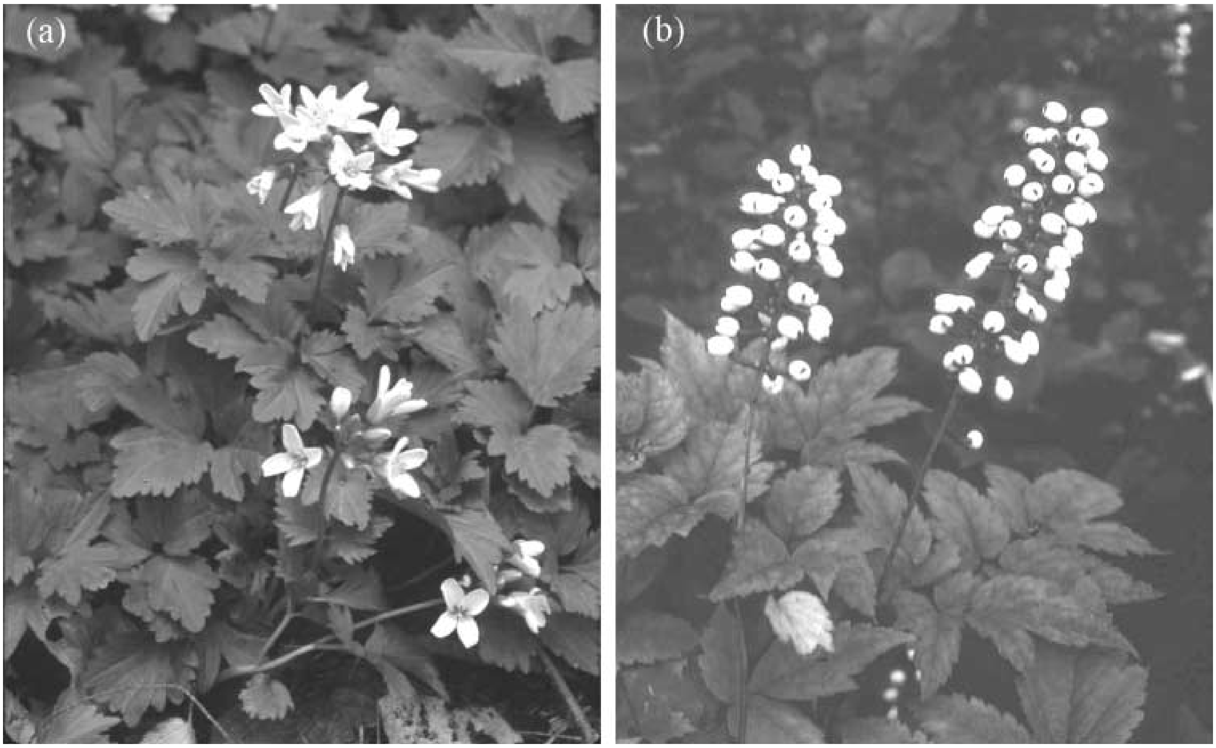

Figure 6 *Cardamine* × *maxima* (a), a sterile, vegetatively reproducing taxon, exhibits a near exclusive association with primary forest, apparently because of the limited effectiveness of clonal spread in colonizing unoccupied sites. In contrast, endozoochores, such as *Actaea alba* (b), have successfully recolonized many secondary forest stands.

For instance, the frequent occurrence of *T. erectum* in nineteenth century secondary stands (66%, the highest frequency of any myrmecochore) is consistent with recent observations that deer may consume and defecate viable seeds of *Trillium* species (M. Vellend, *pers. comm.*). Another myrmecochore, *Sanguinaria canadensis*, is more frequent in secondary forest than in primary, a finding contrary to the results of previous studies (e.g. Matlack, 1994; Jenkins & Parker, 2000). This unusual distribution pattern can be traced to the presence of large populations of *S. canadensis* growing along hedgerows and roadsides in the agricultural and post-agricultural landscapes of the study area, apparently thriving in high light environments (cf. Schemske, 1978; Marino, 1997; Fig. 7). These vigorous populations may have served as prolific seed sources for colonization of secondary stands.

One apparent consequence of limited colonization by clonal herbaceous species (e.g. *A. canadense*, *A. pedatum*) is a ground layer environment that is favourable for the establishment of woody taxa (e.g. *F. americana, Prunus serotina*), which exhibit high species richness and frequency in the herb layer of twentieth century secondary forests and in nineteenth century secondary forest plots more than 50 m from bedrock outcrops. In primary forest, seedlings of woody species probably experience strong competitive pressure from herbaceous taxa that may limit their establishment and growth (Wardle, 1959; Maguire & Forman, 1983). The ability of woody taxa to establish in secondary forests may have long-term effects on the development of the herb layer because of the dense shade produced by the advanced regeneration of trees.

Relict herb populations and colonization dynamics

Because seed rain decreases logarithmically with increasing distance from seed source (Harper, 1977; Willson, 1993), proximity to extant populations is a critical factor controlling the rate and timing of secondary forest colonization. This effect has been widely documented in post-agricultural forests at varying distances from primary stands (Peterken & Game, 1984; Dzwonko, 1993; Matlack, 1994; Brunet *et al.*, 2000). Although our data support this interpretation in areas proximate to primary forest, they also suggest that forest herbs that persisted in local refugia within the agricultural landscape may have had a greater influence on landscape-level colonization dynamics than herb populations in the study area's limited extent of primary forest. Such refugia probably included bedrock outcrops, rocky slopes and hedgerows, where land-use was less intense than in the surrounding landscape (cf. Peterken & Game, 1981; Fritz & Merriam, 1993; Matlack, 1994; Corbit *et al.*, 1999). The effect of local refugia on colonization patterns is most evident in nineteenth century secondary forest, where plots proximate to bedrock outcrops (< 50 m) often exhibit herb

Figure 7 *Sanguinaria canadensis* in bloom along open fence line in early spring (a); detail of densely flowering clone (b), apparently developing in response to high light conditions.

layer composition that is similar to that of primary forest (i.e. including many barochores and myrmecochores), while plots farther from bedrock are significantly less diverse and often lack species with limited dispersal ability (e.g. *C. diphylla, C. caroliniana, A. canadense*). These results suggest that redevelopment of RMF vegetation in secondary forests has proceeded more rapidly where species that are poor dispersers have persisted locally (e.g. on and around bedrock outcrops). Unlike many anemochores and endozoochores, landscape-level interpatch dispersal of myrmecochore and barochore seeds does not appear to be sufficient for successful establishment of these species in secondary forest sites on the time-scale considered by this study. For these taxa, relict populations in the post-agricultural landscape may greatly increase rates of recolonization. While the presence of remnant forest herb populations in agricultural landscapes has been noted previously, the critical role of these relicts for landscape-level species recovery has not been emphasized, perhaps because many studies have investigated regions with on-going agricultural use and limited opportunities for relict populations to expand.

Conservation implications

As a result of high species richness and the occurrence of numerous rare taxa, RMF are a conservation priority throughout the Northeast. Our results suggest that the extent of RMF may have been substantially greater in the past, and that modern RMF sites are remnants of a vegetation type that was fragmented and reduced by widespread nineteenth century agriculture. Despite extensive reforestation over the past century, many secondary forest sites that are environmentally suitable for RMF vegetation do not support the suite of species typical of the community, apparently because of the dispersal limitations of forest herbs with ant-dispersed seed and those with no morphological adaptations for seed dispersal. These poorly dispersed taxa, which are well-adapted for growth in stable forest ecosystems, as indicated by their predominance in the herb layer of primary stands, are maladapted for rapid population recovery and recolonization following their elimination from large portions of the landscape by severe disturbance. This perspective enhances the conservation value of primary forests with large RMF herb populations, as significant natural colonization of secondary forests is unlikely on time scales relevant for present-day conservation efforts. Nonetheless, it should be noted that poorly dispersed forest herbs have persisted in refugia outside primary forest, and these small populations have greatly enhanced landscape-level species recovery during the extensive reforestation of the twentieth century. Protection of secondary forests around such refugia (e.g. bedrock outcrops, hedgerows) could allow for the development of significant RMF sites, given sufficient time. The study results also suggest species reintroduction as a potential management option, as the modern distribution of poorly dispersed taxa may reflect patterns of historical land-use more than the extent of suitable habitat.

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BIOSKETCHES

Jesse Bellemare is currently pursuing a doctorate in the Ecology and Evolutionary Biology Program at Cornell University. The research presented here was conducted as part of the Master's of Forest Science Program at Harvard University's Harvard Forest. His research interests focus on the ecology of forest herbs, principally the roles of environmental and historical factors and species' autecological characteristics in determining distribution and abundance patterns at local and regional scales.

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Appendix 1 Pearson Correlations with Bonferroni significance test for multiple comparisons

Variable	Land use	Ln Bedrock (m)	Moisture	Aspect°	Slope°	C : N ratio	Soil N%	Soil C%	TSI	Ln O layer (cm)	A horizon cm
Land-use	1.000										
Ln Bedrock (m)	−0.125	1.000									
Moisture class	−0.081	0.004	1.000								
Aspect°	0.279	−0.245	−0.143	1.000							
Slope°	−0.131	−0.199	−0.160	0.259	1.000						
C : N ratio	0.009	0.415	−0.006	0.060	0.204	1.000					
Soil N%	−0.007	**−0.613****	0.009	0.199	0.099	**−0.519****	1.000				
Soil C%	0.012	**−0.579****	−0.007	0.220	0.123	−0.347	**0.976****	1.000			
TSI	−0.138	−0.078	0.293	−0.041	−0.006	−0.033	0.089	0.102	1.000		
Ln O layer (cm)	0.011	−0.380	−0.325	0.104	0.229	−0.309	0.246	0.213	−0.214	1.000	
A horizon (cm)	−0.011	0.053	0.245	0.086	0.055	0.128	−0.004	0.010	0.137	**−0.533****	1.000
Soil bulk density	−0.029	**0.535****	0.117	−0.086	−0.137	0.352	**−0.806****	**−0.824****	−0.115	−0.331	0.053
Ln Rock cover percentage	0.041	**−0.489***	0.043	0.368	0.271	−0.162	**0.548****	**0.577****	0.215	0.225	0.128
TEC	−0.075	**−0.561****	−0.035	0.177	0.080	**−0.543****	**0.892****	**0.864****	0.045	0.324	−0.063
Soil pH	−0.247	0.038	0.150	0.048	−0.010	0.089	0.174	0.193	0.118	−0.246	0.324
SMP Buffer pH	−0.271	0.401	0.229	−0.090	0.007	0.345	−0.384	−0.374	0.212	−0.471	0.368
Soil OM%	−0.008	**−0.550****	−0.003	0.193	0.122	−0.359	**0.944****	**0.963****	0.105	0.164	0.019
Soluble sulphur	0.229	−0.252	−0.126	0.157	0.061	−0.253	0.469	**0.473***	−0.005	0.314	−0.177
Ln E.e. P ppm	0.066	−0.143	−0.001	0.135	0.429	−0.140	0.401	0.396	0.199	0.121	0.052
Ln Ca ppm	−0.294	−0.256	0.216	0.122	0.041	−0.267	**0.523****	**0.495***	0.199	−0.130	0.257
Ln Mg ppm	−0.282	−0.264	0.212	0.172	0.128	−0.220	**0.557****	**0.539****	0.259	−0.151	0.289
K ppm	−0.169	−0.247	−0.034	0.248	0.119	−0.242	**0.559****	**0.549****	0.193	−0.015	−0.028
Ln Na ppm	−0.085	−0.055	0.309	0.120	−0.152	−0.207	0.331	0.328	0.195	−0.118	0.012
B ppm	−0.350	−0.292	−0.039	0.196	0.122	−0.343	**0.558****	**0.516****	0.234	−0.042	0.303
Ln Fe ppm	−0.048	−0.038	−0.038	0.100	0.039	−0.079	−0.119	−0.167	−0.062	0.024	−0.014
Ln Mn ppm	0.054	−0.223	0.060	0.147	0.225	−0.232	0.304	0.280	0.273	−0.062	0.152
Ln Cu ppm	−0.248	−0.032	0.216	0.134	−0.065	−0.181	0.405	0.400	0.342	−0.340	0.409
Al ppm	0.368	−0.109	−0.346	0.084	−0.020	0.045	0.019	0.074	−0.285	0.443	−0.453
Ln Clay percentage	0.170	0.432	0.068	0.000	−0.145	0.139	−0.422	−0.427	−0.037	−0.238	−0.030
Silt percentage	0.147	0.062	−0.052	−0.140	−0.217	−0.124	−0.293	−0.328	0.071	0.059	−0.246
Sand percentage	−0.161	−0.138	0.034	0.127	0.223	0.087	0.344	0.377	−0.060	−0.005	0.225

Variable	Bulk Density	Ln Rock cov percentage	TEC	Soil pH	SMP pH	Soil OM%	Soluble Sulphur	Ln E.e. P ppm	Ln Ca ppm	Ln Mg ppm
Bulk density	1.000									
Ln Rock cover percentage	**−0.575****	1.000								
TEC	**−0.827****	**0.493***	1.000							
Soil pH	−0.041	0.021	0.111	1.000						
SMP Buffer pH	**0.491***	−0.232	**−0.518****	**0.705****	1.000					
Soil OM%	**−0.845****	**0.589****	**0.886****	0.176	−0.400	1.000				
Soluble Sulphur	**−0.574****	0.415	**0.505***	−0.384	**−0.554****	0.505*	1.000			
Ln E.e. P ppm	−0.419	0.320	0.356	−0.158	−0.223	0.364	**0.609****	1.000		
Ln Ca ppm	−0.321	0.268	**0.499***	**0.782****	0.400	0.477*	−0.177	0.009	1.000	
Ln Mg ppm	−0.351	0.287	**0.500***	**0.711****	0.357	0.533**	−0.166	0.126	**0.874****	1.000
K ppm	−0.391	0.297	**0.517****	0.372	0.035	0.563*	0.112	0.235	**0.549****	**0.721****
Ln Na ppm	−0.156	0.316	0.322	0.08	−0.124	0.336	0.037	0.027	0.273	0.295
B ppm	−0.407	0.291	**0.564****	**0.572****	0.212	0.494*	0.067	0.208	**0.761****	**0.731****
Ln Fe ppm	0.115	0.006	0.034	**−0.576****	−0.374	−0.109	0.15	0.018	−0.325	−0.261
Ln Mn ppm	−0.181	0.135	0.197	0.286	0.188	0.253	0.1	0.356	0.307	0.454
Ln Cu ppm	−0.164	0.254	0.288	**0.566****	0.432	0.390	−0.055	0.133	**0.640****	**0.753****
Al ppm	−0.223	0.093	0.09	**−0.550****	**−0.676****	0.072	0.408	0.084	**−0.528****	**−0.605****
Ln Clay percentage	**0.515****	−0.369	−0.416	0.016	0.329	−0.409	−0.05	−0.062	−0.149	−0.123
Silt percentage	0.303	−0.244	−0.192	−0.234	−0.077	−0.331	−0.073	−0.156	−0.247	−0.284
Sand percentage	−0.372	0.29	0.248	0.209	0.008	0.375	0.076	0.152	0.247	0.277

Appendix 1 *continued*

Variable	K ppm	Ln Na ppm	B ppm	Ln Fe ppm	Ln Mn ppm	Ln Cu ppm	Al ppm	Ln Clay percentage	Silt percentage	Sand percentage
K ppm	1.000									
Ln Na ppm	0.226	1.000								
B ppm	**0.603****	0.090	1.000							
Ln Fe ppm	−0.064	−0.061	−0.077	1.000						
Ln Mn ppm	0.467	−0.119	0.427	−0.153	1.000					
Ln Cu ppm	**0.532****	0.288	0.594**	−0.154	**0.473***	1.000				
Al ppm	−0.292	0.077	−0.502*	−0.092	−0.404	**−0.597****	1.000			
Ln Clay (%)	−0.102	−0.047	−0.246	−0.014	0.129	0.107	−0.097	1.000		
Silt (%)	−0.203	−0.014	−0.244	0.285	0.150	−0.183	0.019	0.380	1.000	
Sand (%)	0.202	0.015	0.265	−0.258	−0.161	0.141	0.001	**−0.539****	**−0.984****	1.000

* = $P \leq 0.05$, **$P \leq 0.01$. $n = 61$ plots.

Appendix 2

Taxa cited in Fig. 4(b) species ordination: *Actaea* spp., *Acer saccharum, Adiantum pedatum, Allium tricoccum, Arisaema triphyllum, Asarum canadense, Aster divaricatus, Athyrium filix-femina, Athyrium thelypterioides, Betula* cf. *lenta, Cardamine diphylla, Cardamine × maxima, Carex plantaginea, Carex* cf. *swanii, Carya cordiformis, Caulophyllum thalictroides, Circaea lutetiana, Claytonia caroliniana, Dicentra* spp., *Dryopteris intermedia, Dryopteris marginalis, Erythronium americanum, Fraxinus americana, Galium triflorum, Polygonatum pubescens, Polystichum acrostichoides, Prunus serotina, Smilacina racemosa, Solidago caesia, Tiarella cordifolia, Trillium erectum, Viburnum acerifolium.*