Herbaceous species composition and richness of mesophytic cove forests in the southern Appalachians: synthesis and knowledge gaps

Author(s): Katherine J. Elliott James M. Vose Duke Rankin

Source: The Journal of the Torrey Botanical Society, 141(1):39-71. 2014.

Published By: Torrey Botanical Society

DOI: http://dx.doi.org/10.3159/TORREY-D-13-00054.1

URL: http://www.bioone.org/doi/full/10.3159/TORREY-D-13-00054.1

Journal of the Torrey Botanical Society 141(1), 2014, pp. 39–71

Herbaceous species composition and richness of mesophytic cove forests in the southern Appalachians: synthesis and knowledge gaps[1]

Katherine J. Elliott[2]
Coweeta Hydrologic Laboratory, Center for Forest Watershed Science, Southern Research Station,
USDA Forest Service, Otto, NC 28763

James M. Vose
Center for Integrated Forest Science, Southern Research Station, USDA Forest Service, North Carolina
State University, Raleigh, NC 27695

Duke Rankin
National Forest System, USDA Forest Service, Atlanta, GA 30309

ELLIOTT, K. J. (Coweeta Hydrologic Laboratory, Center for Forest Watershed Science, Southern Research Station, USDA Forest Service, Otto, NC 28763), J. M. VOSE (Center for Integrated Forest Science, Southern Research Station, USDA Forest Service, North Carolina State University, Raleigh, NC 27695), AND D. RANKIN (National Forest System, USDA Forest Service, Atlanta, GA 30309). Herbaceous species composition and richness of mesophytic cove forests in the southern Appalachians: synthesis and knowledge gaps. J. Torrey Bot. Soc. 141: 39–71. 2014.—We synthesized the current information on mesophytic cove forests in the southern Appalachians, assessed the range of variation in herb species composition and diversity in stands with different disturbance histories and environmental conditions, identified key knowledge gaps, and suggested approaches to fill these knowledge gaps. The purpose of this synthesis was to provide information to forest managers to help make decisions about conservation assessments and strategies for rich cove forests in the southern Appalachians. An important finding is that no single study or data set can provide conclusive evidence or clear management strategies. However, an overriding conclusion is that the magnitude of impact and the management actions necessary to restore herbaceous communities are directly proportional to the severity of disturbance, current condition (e.g., presence of *Rhododendron*), site heterogeneity, and historical land use (e.g., agricultural activity). These factors plus a host of other stressors (e.g., climate variability, air pollution, invasives) are likely to have a strong influence on the highly variable patterns observed when comparing herbaceous diversity of 'old-growth' or uncut forests to human disturbed forests (e.g., cutting, air pollution, conversion, invasive plants or insects). Results from this review reinforce our premise that factors controlling herbaceous species presence and abundance are highly complex, thus broad generalizations about the impacts of a single factor such as logging should be interpreted with caution. Of the stressors known to affect forest trees (e.g., pests and pathogens, acidic deposition, air pollution, drought, and wind), little to no information exists on how these same stressors will affect herbaceous plants. A limited number of studies have examined the demography or physiology of forest herbs, particularly across all life stages. While the demography of a few genera have been studied (e.g., *Hexastylis*, *Asarum*, *Trillium*, *Arisaema*, *Goodyera*, *Hepatica*), little to no information exists for the majority of woodland herbs. Species identity is important when considering management of rich cove forests. Diversity may increase following canopy disturbances that favor recruitment of early-seral herbaceous species; therefore, simple indices of diversity (H′, S, and E) are not the best measure of recovery in mesophytic rich coves, particularly where shade-adapted 'rich-cove indicator' species have been replaced by these species. Species-specific life histories and the influence of prevailing site conditions are important lines of research for understanding recovery and sustainability of mesophytic rich cove forests.

Key words: disturbance, herbs, indicator species, Liliaceae, rich coves, seed dispersal.

Southern Appalachian deciduous forests are characterized by strong environmental gradients, where heterogeneity operates at fine spatial and temporal scales that influence herb populations and seedling recruitment (Whittaker and Levin 1977, Houle 1994). Hillslope topography generates steep and predictable light and soil moisture gradients, and the composition of herb communities diverges in a consistent manner across topographical positions (Whittaker 1956, Elliott et al. 1997,

---

[1] This study was primarily supported by the USDA Forest Service, Southern Research Station and partially supported by National Science Foundation grant DEB0823293 to the Coweeta LTER program at the University of Georgia. We are grateful to Drs. Diane DeSteven, Mary Anne Sword Sayer and Chelcy Ford Miniat for providing helpful comments on this manuscript. We also acknowledge the valuable contributions of Forest Service staff that provided field and technical assistance.

[2] Author for correspondence, E-mail: kelliott@fs.fed.us

Received for publication August 15, 2013, and in revised form January 18, 2014.

Hutchinson et al. 1999, Albrecht and McCarthy 2009). Differences in the spatial distributions of forest herbs across topographic moisture gradients and forest floor microenvironments are well described and are assumed to reflect niche differentiation (Beatty 2003, Vellend et al. 2007).

Mesic forest herbs are typically found in concave drainage areas (coves) or riparian areas where soil moisture is higher than in the upland forests found on convex slopes and well drained soils. Mesophytic cove forests can be further differentiated into 'acidic' or 'rich' coves based on their soil nutrient availability and presence/absence of evergreen species such as *Tsuga canadensis* L. and *Rhododendron maximum* L. (Schafale and Weakley 1990, Simon et al. 2005). NautureServe (http//:www.natureserve.org/explorer) also distinguishes Appalachian cove forests based on their acidity, "The system includes a mosaic of acidic and 'rich' coves that may be distinguished by individual plant communities based on perceived differences in soil fertility and species richness (rich examples have higher diversity and density in the herbaceous layer)," and further classifies acidic coves in the southern Appalachians as Typic Type (*Liriodendron tulipifera* L. - *Betula lenta* L. - *Tsuga canadensis*/*Rhododendron maximum* forest) or Silverbell Type (*Tsuga canadensis* - *Halesia tetraptera* Ellis - (*Fagus grandifolia* Ehrh., *Magnolia fraseri* Walter)/*Rhododendron maximum*/*Dryopteris intermedia* (Muhl. ex Willd.) A. Gray forest). In addition, NatureServe provides many more classifications for mesophytic 'rich' cove forest associations (e.g., *Liriodendron tulipifera* - *Quercus rubra* L. - *Magnolia acuminata*/*Cornus florida* L. forest, *Liriodendron tulipifera* - *Fraxinus americana* L. - (*Tilia americana* L., *Aesculus flava* Aiton)/*Actaea racemosa* L. - *Laportea canadensis* (L.) Weddell forest). While acidic coves and rich coves have similar landform, underlying geology and topographic moisture condition, they differ primarily based on their limited soil fertility and light availability under a dense evergreen cover (Ulrey 2002). Acidic cove forests have lower pH levels and soil base saturation (sum of Ca, Mg, and K) and a higher abundance of evergreen species than rich cove forests. Acidic cove forests with *Rhododendron* canopy cover have a limited number of forest herbs (low richness) with extremely low abundance (density or cover) compared to forests without *Rhododendron* (Newell and Peet 1997, Ulrey 2002). By definition, rich cove forests have ≤ 25% canopy coverage of *T. canadensis* and ≤ 10% coverage of evergreen shrubs (*R. maximum*, *Kalmia latifolia* L.; Schafale and Weakley 1990, Newell and Peet 1997).

Herb layer vegetation is also affected by natural and anthropogenic disturbances including individual tree falls, catastrophic wind events, catastrophic fire, and timber harvesting that increase light and expose mineral soil (Gilliam and Roberts 2003, Small and McCarthy 2005, Elliott et al. 2011, Belote et al. 2012). Some studies suggest that late-seral, shade-adapted herbs re-colonize forest stands that are recovering from broad-scale disturbances, such as logging and agriculture of the late 19th to early 20th centuries (Gilliam and Roberts 2003, Gilliam 2006, Gilliam 2007, Vellend et al. 2007); thus, post-dispersal demographic processes partially explain why species-environment relationships become increasingly important in shaping forest plant distributions.

Two recent studies (Jackson et al. 2009, Wyatt and Silman 2010) have examined the long standing debate concerning herbaceous diversity recovery of secondary, post-logging forests to an old-growth forest condition, particularly mesophytic rich coves of the southern Appalachians (Greenlee 1974, Duffy and Meier 1992, Meier et al. 1995). The two studies reported contrasting conclusions. Wyatt and Silman (2010) found higher species richness in old-growth forests (> 150-year-old) than mature forests (100–140-year-old) last logged between 1864 and 1906. Jackson et al. (2009) found minor compositional differences between old growth (> 125-year-old) and secondary (70–80-year-old) rich coves, but no significant differences in richness or diversity as measured by Shannon's H' index. Both studies used recognized criteria for mixed-mesophytic old-growth (Greenberg et al. 1997, Hardt and Swank 1997, McCarthy 2003) as a guide for site selection, and both selected their sites from the 'rich cove hardwood' forest type as defined by USDA Forest Service Continuous Inventory and Stand Condition data. Some of the disparity between studies may be due to methods. For example, the age ranges for mature secondary forests in Wyatt and Silman (2010) overlapped the age ranges of old-growth stands in Jackson et al. (2009). The two studies also differed in the number of sites sampled: Jackson et al. (2009) analyzed a total of 26 sites (13 old-growth and 13 secondary stands) within the Nantahala and Pisgah National Forests, whereas Wyatt and Silman (2010) analyzed only 6 sites (3 old-growth and 3 secondary stands) within the Nantahala National Forest. Other factors such as variation among sites in gap dynamics, microclimate, soil physical and chemical properties, and micro-topography (e.g., pits and mounds) may also explain the disparity of findings. In short, whether mesophytic rich coves of old-growth forests have greater herbaceous diversity than secondary forests remains an unsettled question.

Since there are so few 'virgin' forests (i.e., forest preserves or natural areas with no logging history) in the southern Appalachians, the debate over factors regulating herbaceous diversity in old-growth vs. mature secondary forests is likely to remain unresolved using traditional sampling and empirical analyses because adequate replication is not possible. As an alternative, we propose an approach that examines variation in cove forest understory diversity across a range of disturbances and environmental conditions. We hypothesize that this approach can better answer the question: what controls herbaceous diversity in mesophytic cove forests in the southern Appalachians? To accomplish this, we: (1) synthesized the current information on mesophytic cove forests in the southern Appalachians (including some examples from the central Appalachians); (2) assessed the range of variation in herb species composition and diversity in stands with different disturbance histories and environmental conditions; and (3) identified key knowledge gaps and suggested approaches to fill those knowledge gaps. We expect that this synthesis paper will provide information to forest managers to make decisions about conservation assessments for rich cove forests in the southern Appalachians.

Methods and Approach. We reviewed and synthesized literature centered on studies from rich cove forests in the southern Appalachians. We compiled available reports and publications on herbaceous-layer of mesophytic cove forests from a database of scientific literature (Web of Science), an internet search engine (Google), and additional references in these sources, searching with keyword combinations of 'forest herbs, mesophytic, rich coves, invasive, plant demography, Appalachians.' We compiled studies of herbaceous-layer response to disturbance in eastern deciduous forests, where abundance (cover or mass), species richness (S), diversity (Shannon H′ index), and evenness (E) were recorded (Table 1). We also included data collected from managed and unmanaged watersheds in the Coweeta Basin, western North Carolina (Table 2). We used only the herbaceous-layer sampling from the rich cove portions of these watersheds for comparisons.

We considered using meta-analysis (Rosenberg et al. 2000), which requires means, standard deviations, and numbers of replicates, to compare S and H′ for the herbaceous-layer studies found in our literature review. However, after further examination, the disparity among studies in methodology (e.g., sample size, unit area sampled, extent of sampling, inclusion of woody species, standard deviations not reported) limited our ability to use this analysis (Table 1). We concur with other critiques of meta-analyses that the apparent lack of generality in species richness and disturbance might simply reflect methodological inconsistencies among field studies (Whittaker 2010). Because of the strong effects of area and heterogeneity on richness (Small and McCarthy 2002), such differences in scale and methodology can confound cross-study comparisons (Adler et al. 2001). For example, Paillet et al. (2010) conducted a meta-analysis of biodiversity differences between managed and unmanaged forests in Europe. Their literature search found only 47 papers across temperate and boreal forests representing studies conducted between 1978 and 2007, and they accepted forests that had not been managed for at least 20 years as 'unmanaged.' They reported a low significance level for differences between managed and unmanaged forests and provided several explanations, including a lack of control of confounding factors in the sampling design and the use of total species richness for analysis. They concluded that it would be more meaningful to focus on species traits and analyze the species richness of ecological or functional groups. Similarly, they concluded that it would be interesting to focus on species composition and determine which species are more prevalent in unmanaged forests than in managed forests.

To do that type of comparison, one would need the original data sets that are not

Table 1. Herbaceous-layer richness (S), diversity (H′, Shannon's index of diversity) and evenness (E, Pielou's evenness index) of Eastern deciduous forests stands. Herbaceous-layer includes woody species ≤ 1.0 m height. † = reference stand for the cited study. Values in parentheses are standard errors.

Location	Latitude, longitude	Elevation (m)	Stand age (years)	Study Area Size (ha)	Community	Stand Treatment	Cover (%) or biomass (g/m²)	Diversity [a]			Citation
								S (#/m²)	H′	E	
Coweeta, western NC WS7	35°04′ N, 83°26′ W	720–950	50	24	Mixed deciduous	Mature, pre-cut	–	16.1 (1.3)	2.11 (0.10)	0.79 (0.02)	Elliott et al. 1997 [b]
Coweeta, western NC WS7	35°04′ N, 83°26′ W	720–950	1	24	Mixed deciduous	Clearcut	38.6 g/m² (10.6)	3.4 (0.4)	0.87 (0.12)	0.81 (0.03)	Elliott et al. 1997 [b]
Coweeta, western NC WS7	35°04′ N, 83°26′ W	720–950	17	24	Mixed deciduous	Post-clearcut	4.1 g/m² (1.4)	3.7 (0.5)	0.72 (0.11)	0.67 (0.04)	Elliott et al. 1997 [b]
Coweeta, western NC WS7	35°04′ N, 83°26′ W	720–950	30	24	Mixed deciduous	Post-clearcut	12.4 g/m² (5.2)	10.4 (1.2)	1.22 (0.17)	0.52 (0.05)	Elliott, unpublished
Coweeta, western NC WS14	35°03′ N, 83°25′ W	700–900	70	14	Mixed deciduous	Mature forest†	–	13.3 (1.9)	1.66 (0.15)	0.70 (0.04)	Elliott et al. 1998 [b]
Coweeta, western NC WS6	35°03′ N, 83°25′ W	700–900	1	9	Mixed deciduous	Grass-to-forest	490 g/m² (105)	5.6 (0.4)	0.69 (0.08)	0.42 (0.04)	Elliott et al. 1998 [b]
Coweeta, western NC WS6	35°03′ N, 83°25′ W	700–900	28	9	Mixed deciduous	Grass-to-forest	51.0 g/m² (6.5)	12.1 (0.7)	1.16 (0.08)	0.47 (0.03)	Elliott et al. 1998 [b]
Coweeta, western NC WS34	35°04′ N, 83°28′ W	1220–1370	70+	6	Red oak/red maple/hickory	Mature forest†	23.9% (3.2)	9.5 (1.0)	1.49 (0.14)	0.70 (0.04)	Elliott et al. 2002 [b]
Coweeta, western NC WS34	35°04′ N, 83°28′ W	1220–1370	2	10	Red oak/red maple/hickory	Wind then salvage	103.6% (3.2)	14.5 (0.7)	1.87 (0.07)	0.71 (0.02)	Elliott et al. 2002 [b]
Coweeta, western NC WS28	35°03′ N, 83°25′ W	1030–1140	70	32	Yellow poplar	Mature, thinned in 1963	36.2% (4.3)	30.4 (2.2)	2.15 (0.08)	0.64 (0.02)	Parr 1992 [c]
Wine Spring, western NC	35°15′ N, 83°35′ W	1380–1580	125+	4.0–6.5	Red oak/red maple/chestnut oak	Mature, Uncut	100% (19)	15.0 (0.7)	2.12 (0.06)	0.79 (0.01)	Elliott and Knoepp 2005 [b]
Wine Spring, western NC	35°15′ N, 83°35′ W	1380–1580	2	4.0–6.5	Red oak/red maple/chestnut oak	Two-aged	107% (11)	14.9 (0.8)	2.12 (0.08)	0.80 (0.02)	Elliott and Knoepp 2005 [b]

Table 1. Continued.

Location	Latitude, longitude	Elevation (m)	Stand age (years)	Study Area Size (ha)	Community	Stand Treatment	Cover (%) or biomass (g/m^2)	Diversity[a] S (#/m^2)	Diversity[a] H′	Diversity[a] E	Citation
Wine Spring, western NC	35°15′ N, 83°35′ W	1380–1580	2	4.0–6.5	Red oak/red maple/ chestnut oak	Group	105% (9)	16.8 (0.7)	2.25 (0.07)	0.81 (0.02)	Elliott and Knoepp 2005[b]
Wine Spring, western NC	35°15′ N, 83°35′ W	1380–1580	2	4.0–6.5	Red oak/Red maple/ chestnut oak	Shelter-wood	123% (8)	18.8 (0.8)	2.40 (0.06)	0.82 (0.01)	Elliott and Knoepp 2005[b]
Ray Branch, Western NC	35°06′ N, 83°06′ W	850–950	60+	4 sites	Mixed deciduous	Mature forest†	50.6% (3.5)	11.0 (0.5)	1.89 (0.07)	0.80 (0.02)	Elliott, unpublished
Ray Branch, western NC	35°06′ N, 83°06′ W	850–950	2	4 sites	Mixed deciduous	Two-age cut	100.4% (5.4)	17.2 (0.6)	2.42 (0.04)	0.86 (0.01)	Elliott, unpublished
Chatta-hoochee NF, northern GA	–	740–1120	15	3 sites	Cove hardwoods/ poplar	Clearcut	–	37.0 (6.6)	3.14 (0.12)	0.89 (0.01)	Ford et al. 2000[d]
Chatta-hoochee NF, northern GA	–	740–1120	25	3 sites	Cove hardwoods/ poplar	Clearcut	–	35.3 (2.0)	3.07 (0.06)	0.87 (0.01)	Ford et al. 2000[d]
Chatta-hoochee NF, northern GA	–	740–1120	50	3 sites	Cove hardwoods/ poplar	Heavy selection cut	–	42.7 (4.1)	3.19 (0.17)	0.86 (0.02)	Ford et al. 2000[d]
Chatta-hoochee NF, northern GA	–	740–1120	>85	4 sites	Cove hardwoods/ poplar	Mature forest†	–	43.7 (3.0)	3.18 (0.16)	0.85 (0.02)	Ford et al. 2000[d]
GSMNP[e]; western NC	35°37′ N 83°31′ W	287–975	70+	6 sites	Oak/hickory	Mature forest†	22.3% (6.0)	22 (3)	2.4 (0.2)	0.74 (0.02)	Holzmueller et al. 2009
GSMNP[e]; western NC	35°37′ N 83°31′ W	287–975	70+	7 sites	Oak/hickory	R_x fire (single R_x)	33.4% (5.5)	27 (2)	2.5 (0.2)	0.75 (0.03)	Holzmueller et al. 2009
GSMNP[e]; western NC	35°37′ N 83°31′ W	287–975	70+	4 sites	Oak/hickory	R_x fire (2×, repeated)	24.0% (7.5)	27 (4)	2.3 (0.3)	0.70 (0.03)	Holzmueller et al. 2009
GSMNP[e]; western NC	35°37′ N 83°31′ W	287–975	70+	3 sites	Oak/hickory	R_x fire (3×, repeated)	26.7% (9.2)	27 (5)	2.0 (0.4)	0.62 (0.05)	Holzmueller et al. 2009

Table 1. Continued.

Location	Latitude, longitude	Elevation (m)	Stand age (years)	Study Area Size (ha)	Community	Stand Treatment	Cover (%) or biomass (g/m^2)	Diversity [a]			Citation
								S ($\#/m^2$)	H′	E	
GSMNP[e]; Cades Cove, JO-site	35°37′ N 83°31′ W	520–680	~100	~100	White oak/ tulip poplar	Deer exclosure	17.2% (5.8)	14.2 (1.2)	2.1 (0.1)	0.8 (0.1)	Griggs et al. 2006
GSMNP[e]; Cades Cove, JO-site	35°37′ N 83°31′ W	520–680	~100	~100	White oak/ tulip poplar	Control†	5.9% (2.9)	18.4 (3.7)	2.4 (0.2)	0.7 (0.1)	Griggs et al. 2006
GSMNP[e]; Cades Cove, HL-site	35°37′ N 83°31′ W	520–680	~100	~100	White oak/ hemlock	Deer exclosure	42.6% (21.6)	5.6 (0.9)	0.8 (0.2)	0.5 (0.1)	Griggs et al. 2006
GSMNP[e]; Cades Cove, HL-site	35°37′ N 83°31′ W	520–680	~100	~100	White oak/ hemlock	Control†	45.0% (17.6)	6.2 (1.8)	0.4 (0.1)	0.2 (0.1)	Griggs et al. 2006
GSMNP[e]; Cades Cove, AC-site	35°37′ N 83°31′ W	520–680	~100	~100	Sweetgum/ tulip poplar	Deer exclosure	48.0% (21.2)	14.0 (1.3)	1.7 (0.2)	0.6 (0.1)	Griggs et al. 2006
GSMNP[e]; Cades Cove, AC-site	35°37′ N 83°31′ W	520–680	~100	~100	Sweetgum/ tulip poplar	Control†	53.6% (9.7)	11.8 (0.8)	1.3 (0.0)	0.5 (0.0)	Griggs et al. 2006
southern Appalachians western NC	35°–32° N, 83°–84° W	1070–1370	70	13 sites	Tulip poplar/ cherry/red oak	Mature forest	168%	9.8	1.91	–	Jackson et al. 2009
southern Appalachians western NC	35°–32° N, 83°–84° W	1070–1370	125–300	13 sites	Tulip poplar/ cherry/red oak	Old-growth	197%	9.3	1.68	–	Jackson et al. 2009
southern Appalachians western NC	Nantahala National Forest	700–1200	>150	3 sites	Mesophytic cove, deciduous	Old-growth	–	9.8 (0.2)	–	–	Wyatt and Silman 2010 [f]
southern Appalachians western NC	Nantahala National Forest	700–1200	100–150	3 sites	Mesophytic cove, deciduous	Mature forest	–	7.4 (0.2)	–	–	Wyatt and Silman 2010 [f]
Cumberland Plateau; KY	37°05′ N, 83°00′ W	320–600	>100	52	Mesophytic cove, deciduous	Old-growth	68%	10.2 (0.5)	1.5 (0.2)	0.68 (0.02)	McEwan and Muller 2011
Alleghany Plateau, OH	38°43′–39° N, 82°23′–41′ W	210–280	100+	75–80	Oak/hickory	Mature forest†	–	14.9 (0.7)	3.73 (0.04)	0.91 (0.01)	Hutchinson et al. 2005 [c]

Table 1. Continued.

Location	Latitude, longitude	Elevation (m)	Stand age (years)	Study Area Size (ha)	Community	Stand Treatment	Cover (%) or biomass (g/m^2)	Diversity [a]			Citation
								S (#/m^2)	H′	E	
Alleghany Plateau, OH	38°43′–39° N, 82°23′–41′ W	210–280	100+	75–80	Oak/hickory	R_x fire (repeated)	–	17.9 (0.9)	3.82 (0.03)	0.92 (0.01)	Hutchinson et al. 2005 [c]
Alleghany Plateau, OH	38°43′–39° N, 82°23′–41′ W	210–280	100+	75–80	Oak/hickory	R_x fire (annual)	–	18.3 (0.8)	3.81 (0.03)	0.91 (0.01)	Hutchinson et al. 2005 [c]
Morgan-Monroe SF; south central, IN	39°32′ N, 86°41′ W	275	60–80	9733	Sugar maple/ tulip poplar/ white & black oak	Control	36.7% (17.4); 24.7 g/m^2 (10.8)	9.7 (2.6)	–	–	Welch et al. 2007
Alleghany Plateau, OH	39°21′ N, 82°03′ W	–	100+	–	Mixed-mesophytic	Control†	67.9%	30.7	2.92	–	Harrelson and Matlack 2006 [g]
Alleghany Plateau, OH	39°21′ N, 82°03′ W	–	34–41	–	Mixed-mesophytic	Abandoned pasture	124.9%	34.3	3.02	–	Harrelson and Matlack 2006 [g]
Northwest PA	41°30′–48′ N, 78°44′–79°10′ W	500–700	–	6.5–8.0	Black cherry/ red maple	Herbicide/ Shelter-wood	–	21.5 (1.2)	2.11 (0.13)	0.70 (0.05)	Ristau et al. 2011 [c]
Northwest PA	41°30′–48′ N, 78°44′–79°10′ W	500–700	–	6.5–8.0	Black cherry/ red maple	Control	–	21.5 (1.3)	1.98 (0.15)	0.65 (0.04)	Ristau et al. 2011 [c]
North-central WV	39°03′ N, 79°49′ W	735–860	25	34	Mixed deciduous	Treated; 25-yr-old clearcut	14.5% (2.0)	16.5 (2.0)	2.3 (0.15)	8.2 (0.1)	Gilliam et al. 2006 [h]
North-central WV	39°03′ N, 79°49′ W	750–875	>90	38	Mixed deciduous	Control	12.5% (3.0)	14.6 (2.2)	2.1 (0.20)	8.1 (0.3)	Gilliam et al. 2006 [h]
Wayne County, WV	38°31′ N, 82°42′ W	200	1	1.0	*Festuca elatior*, *Aster pilosus*	Pasture	180% (6)	5.9 (0.2)	1.38 (0.03)	0.78 (0.01)	Gilliam and Dick 2010
Wayne County, WV	38°31′ N, 82°42′ W	200	1	1.0	*Poa*, *Ambrosia*	Old-field	256% (12)	13.4 (0.5)	2.21 (0.05)	0.86 (0.01)	Gilliam and Dick 2010

Table 1. Continued.

Location	Latitude, longitude	Elevation (m)	Stand age (years)	Study Area Size (ha)	Community	Stand Treatment	Cover (%) or biomass (g/m²)	Diversity [a] S (#/m²)	H′	E	Citation
Allegheny Plateau, OH	39°21′ N, 86°16′ W	320	>125	1.7	Mixed-oak	Mature forests [reference]	–	4.7 (0.4)	1.08 (0.09)	–	Small and McCarthy 2005
Allegheny Plateau, OH	39°21′ N, 86°16′ W	320	10	1.7	Mixed-oak	Clearcuts	–	6.0 (0.4)	1.34 (0.07)	–	Small and McCarthy 2005
Southwest Ohio	39°30′ N, 84°45′ W	–	55	1.0	Sugar maple/ash/black cherry	Non-invaded	–	19.0 (1.9)	–	–	Hartman and McCarthy 2008
Southwest Ohio	39°30′ N, 84°45′ W	–	55	1.0	Sugar maple/white ash	Invaded with *Lonicera maackii*	–	18.2 (1.0)	–	–	Hartman and McCarthy 2008
Somerset County, NJ, Piedmont	40°30′ N, 74°34′ W	3–76	100–150	2.5–3.9	Red oak/ash/white & black oak	With *M. vimimeum*	–	4.9 (0.4)	–	–	Aronson and Handel 2011
Somerset County, NJ, Piedmont	40°30′ N, 74°34′ W	3–6	100–150	2.5–3.9	Red oak/ash/white & black oak	Without *M. vimimeum*	–	6.5 (0.4)	–	–	Aronson and Handel 2011
Shawnee Hills, IL	37°20′–24′ N, 89°19′–22′ W	100–500	Mature 70–80	105–369	Dry to mesic oak	1996–98	13.1% (2.6)	–	–	–	Chandy et al. 2009
Shawnee Hills, IL	37°20′–24′ N, 89°19′–22′ W	–	Mature 70–80	105–369	Dry to mesic oak	2001–02	22.6% (3.7)	–	–	–	Chandy et al. 2009
Ozark Hills, IL	37°14′–33′ N, 88°07′–31′ W	100–500	Mature 70–80	7–83	Dry to mesic oak	1996–98	17.8% (1.3)	–	–	–	Chandy et al. 2009
Ozark Hills, IL	37°14′–33′ N, 88°07′–31′ W	–	Mature 70–80	7–83	Dry to mesic oak	2001–02	24.5% (2.0)	–	–	–	Chandy et al. 2009
Indiana	39°13′ N, 86°32′ W	150	Mature 50–60	0.4	Bottomland hardwoods, boxelder, tulip poplar	With *M. vimimeum*	578 g/m² (6)	8.0 (0.5)	1.4 (0.1)	0.57 (0.05)	Flory and Clay 2010
Indiana	39°13′ N, 86°32′ W	150	Mature 50–60	0.4	Bottomland hardwoods, boxelder, tulip poplar	Without *M. vimineum*	367 g/m² (4)	16.0 (1.0)	1.8 (0.1)	0.64 (0.03)	Flory and Clay 2010

Table 1. Continued.

Location	Latitude, longitude	Elevation (m)	Stand age (years)	Study Area Size (ha)	Community	Stand Treatment	Cover (%) or biomass (g/m²)	Diversity [a]			Citation
								S (#/m²)	H′	E	
Upper peninsula, MI	46°37′ N, 88°29′ W	411–448	Uneven aged 50 +	235	Sugar maple/ red maple/ yellow birch	Gap opening (0.12 ha)	49.3% (1.0)	20.6 (0.8)	2.46 (0.06)	0.81 (0.01)	Shields and Webster 2007
Upper peninsula, MI	46°37′ N, 88°29′ W	411–448	Mature 50 +	235	Sugar maple/ red maple/ yellow birch	Control	29.7% (0.6)	12.2 (0.9	1.80 (0.1)	0.71 (0.02)	Shields and Webster 2007

[a] Shannon-Wiener index was calculated as: $H' = p_i (\ln p_i)$, where p_i = proportion of total percent cover or total aboveground biomass (g) of species i. Species evenness was calculated as: $E = H'/H'_{MAX}$, where H'_{MAX} = maximum level of diversity possible within a given population = ln(number of species) (Magurran 2004).

[b] S, H′, and E were re-calculated at a finer spatial scale (1.0 m² plot) than presented in the original manuscripts (≥ 100 m² plot) for comparisons among other studies listed.

[c] Hutchinson et al. (2005) used a 2.0 m² plot for herbaceous layer sampling. Ristau et al. (2011) and Parr (1992) used a 4.0 m² area (4*1.0 m²) for S, H′, and E.

[d] Ford et al. (2000) calculated S, H′, and E based on percent occurrence for 60-0.25 m² plots in each site.

[e] Great Smoky Mountains National Park, western NC.

[f] Wyatt and Silman (2010) species richness is S per 0.25 m² plot. Not possible to reconstruct H′ and E from presentation of data.

[g] Harrelson and Matlack (2006) calculated S and H′ based on a 0.008 ha circular plot.

[h] Gilliam and others (2006) calculated S, H′, and E based on a 0.04 ha plot.

Table 2. Watersheds within Coweeta Basin with herbaceous-layer data. Elevation range refers to the mesophytic cove area within each watershed.

Watershed	Treatment description and measurements	Location
WS13	All woody vegetation cut in 1939 and allowed to re-grow until 1962 when the watershed was again clearcut; no products removed in either treatment. Vegetation re-measured in 1982 and 1992.	Low elevation (700–850 m), east-facing.
WS6	Clearcut in 1958, products removed and remaining residue piled and burned. Surface soil scarified, watershed planted to grass, limed and fertilized in 1959; fertilized again in 1965. Grass herbicide-treated in 1966 and 1967; watershed subsequently reverted to successional vegetation. Vegetation was measured several times; last measured in 1995 and 2013.	Low elevation (700–850 m), north-facing.
WS7	Lower portion of watershed grazed by six cattle during a 5-month period each year from 1941 to 1952. Commercially clearcut and cable logged in 1977. Permanent plots measured in 1974, 1977, 1979, 1984, 1993, 1997, and 2008.	Low elevation (720–900 m), south-facing.
WS28	Multiple-use demonstration comprised of commercial harvest on 77 ha upper slope and thinning on 39 ha of the cove forest in 1963; and no cutting on 28 ha. Permanent plots measured before treatment and last measured in 1991.	High elevation (950–1140 m), east-facing.
WS34	Reference, high elevation (> 1100 m), mixed-oak; and ~10 ha windthrowed then salvage-logged in 1995–96. Measured in 1996 and 1997.	High elevation (> 1100 m), east-facing.
WS14	Reference, low elevation, north-facing with mixed hardwoods remaining undisturbed since 1923. Last measured in 1993.	Low elevation (700–950 m), north-facing.
Reynolds	Reference, low elevation, north-facing with mixed hardwoods remaining undisturbed since 1923.	Mid elevation (930–960 m), north-facing.

* Coweeta Basin is located in the Nantahala Mountain Range of western North Carolina, USA, within the Blue Ridge Physiographic Province, near the southern end of the Appalachian Mountain chain (latitude 35°03′ N, longitude 83°25′ W). Slopes are steep ranging from 30 to over 100 percent. Soils are deep sandy loams and are underlain by folded schist and gneiss. Two soil orders are found within Coweeta, immature Inceptisols and older developed Ultisols (Thomas 1996). Streams flow throughout the year, fed by approximately 1800 mm of precipitation per year, most of which is rain. Mean annual temperature is 12.6 °C and ranges from an average of 3.3 °C in January to 21.6 °C in July. Frequent rain, more than 130 storms distributed throughout the year, sustains high evapotranspiration rates and a humid climate (Laseter et al. 2012).

available from the compiled literature synthesis. Therefore, to supplement our approach, we compared original data sets collected in rich cove forests within the Coweeta Basin, western North Carolina (Table 2). We used multiple comparison tests in PROC GLM, SAS 9.3 (SAS Institute, Cary, NC) to determine differences in S and H′ among Coweeta watersheds.

The reviewed literature used the terms: 'late-seral species,' 'forest herbs,' 'shade-tolerant species,' 'shade-adapted species,' and 'closed-canopy species' interchangeably or synonymously. The later three refer to an environmental condition where a particularly suite of species exist or even thrive under a closed forest canopy. The term 'late-seral' is based on forest succession theory (e.g., Kimmins 1997), where time since disturbance is denoted by early-, mid-, and late-seral and the length of time of the seral-stages is dependent on a variety of factors. To our knowledge, there is no consensus among plant ecologists as to how to classify herbaceous species into early-, mid- and late-seral categories. One approach is to define early-seral herb species as those that are adapted to grow under high light conditions (i.e., shade-intolerant); whereas, late-seral herbs are those that are adapted to grow under low light conditions (i.e., shade-tolerant, typically found beneath closed canopy forests). For the purposes of this review and to avoid confusion, we use the term shade-adapted and denote the original authors' terminology in parentheses such as (= "late-seral") or (= "closed-canopy"). We also discuss the importance of shade-adapted species as indicators of mesophytic rich coves. For all studies reviewed here, species nomenclature follows Gleason and Cronquist (1991).

Results and Discussion. OVERVIEW OF HERBACEOUS-LAYER RESPONSES TO DISTURBANCE. Numerous studies have been conducted in the central and southern Appalachians on response of the 'herbaceous-layer' (i.e., herbs plus woody plants in the ground layer) to disturbance (Table 1). In general, herbaceous-layer response varies with the type and severity of the disturbance, but also differs among ecoregions and forest types within the Appalachians (see Elliott et al. 2011 for review). The most severe disturbances that remove topsoil (e.g., mining) or disrupt surface soils (e.g., agriculture) require the longest time to recover and may never recruit shade-adapted (= "late-seral") herbs without aggressive management such as preparing suitable habitat and introducing seeds or seedlings (Hall et al. 2010). Less severe disturbances, such as logging and fire, may not reduce species richness or diversity, but species composition or abundance may be altered (e.g., Hutchinson et al. 2005, Chandy et al. 2009, Holzmueller et al. 2009). Wildland fire (wild and prescribed) is not likely to have a strong influence in mesophytic rich coves, so it will not be discussed as a disturbance agent in this review.

In the central Appalachians, Small and McCarthy (2005) compared ~7-yr-old clearcut stands and mature (> 125 years old), second growth stands in Ohio. All measures of herb abundance and diversity were greater in clearcut relative to mature stands, including mean cover (10.94 ± 1.42 versus 4.89 ± 0.57), S, and H′ (Table 1). Clearcut and mature forests shared several shade-tolerant, perennial species, including *Aster divaricatus* L., *Amphicarpaea bracteata* (L.) Fernald, *Carex digitalis* Willd., *Lysimachia quadrifolia* L., *Polystichum acrostichoides* (Michx.) Schott, and *Viola sororia* Willd. Younger stands showed greater importance of annual species or shade-intolerant graminoids, such as *Carex laxiflora* Lam., *Panicum (Dichanthelium) clandestinum* L., and *Poa* spp. and non-native herbs (e.g., *Cardamine hirsuta* L. and *Potentilla recta* L.); whereas, mature stands showed greater importance of shade-tolerant perennials, including *Cimicifuga racemosa* (L.) Nutt., *Osmorhiza claytonii* (Michx.) C. B. Clarke, *Polygonatum pubescens* (Willd.) Pursh, *Smilacina racemosa* (L.) Desf., and *Uvularia perfoliata* L. (Small and McCarthy 2005).

Belote et al. (2009) investigated how a gradient in disturbance intensity caused by different levels of timber harvesting influenced herbaceous-layer diversity through time and across spatial scales ranging from 1 m^2 to 2 ha. The gradient of tree canopy removal and associated forest-floor disturbance ranged from clearcut (95% basal area removed), leave-tree harvest (74% of basal area removed but leaving a few dominants), shelterwood harvest (56% of basal area removed), herbicide-treated understory (removal of suppressed trees via basal application of herbicide), to uncut control. In the first year after disturbance, species richness increased at both spatial scales, but after ten years of forest development, canopy effects once again controlled the understory (Belote et al. 2009) and differences in species richness among harvest intensities were no longer apparent. In a companion paper, Belote et al. (2012) found that species composition shifted following harvesting, with ephemeral colonizers being abundant in the first year after disturbance, and then being extirpated after ten years with canopy closure. Colonizers included *Erechtites hieraciifolia* (L.) Raf. ex DC., *Potentilla* spp., *Hieracium* spp., *Lobelia inflata* L., *Solidago* spp., *Symphyotrichum* spp., and *Phytolacca americana* L.

Ford et al. (2000) surveyed herbaceous plants (excluding ferns) in 15-, 25-, 50-, and > 85-year-old cove-hardwood forests in northern Georgia (Table 1). They did not find differences in S, H′, or E among stand ages (Table 1); however, they did find that some herb species were more abundant in one stand age than in others. Specifically, of 69 species and/or genera of herbaceous flora recorded, four species' abundances significantly differed among stand ages. *Disporum lanuginosum* (Michx.) G. Nicholson was more abundant in older stands than in younger stands. *Tiarella cordifolia* L. was absent in 25-year-old stands, but common in 15-, 50-, and > 85-year-old stands, and *Lysimachia quadrifolia* and *Potentilla canadensis* L. were more common in 25-year-old stands than in older stands and 15-year-old stands. Other species were either uncommon or found in only one stand age; thus, a statistical test could not be performed (see Ford et al. 2000, page 242). No species was exclusive to the > 85-year-old stand. Based on their results, Ford et al. (2000) concluded that landscape measures such as patch size or extent of similar habitat, and connectivity to other suitable patches or habitats should be considered when assessing herbaceous community recovery rate following disturbances such as forest management activities.

Habitat fragmentation and patch size have been noted as important factors limiting cove forest species abundance. For example, Pearson et al. (1998) examined 17 shade-adapted (= "closed canopy, mesic") species, and they found that large forest patches contained greater abundance of shade-adapted species than small patches. Fraterrigo et al. (2009a) found that habitat connectivity had large effects on population size of shade-adapted (= "forest herbs") species.

The benefit of connectivity to recovery of mesophytic rich cove vegetation was addressed by Bellemare et al. (2002) who found that herbaceous-layer richness did not differ significantly among old-growth and post-agriculture secondary stands. Their results suggested that the extent of mesophytic rich forests may have been substantially greater in the past, and that modern sites are remnants of a vegetation type that was fragmented and reduced by widespread 19th century agriculture. Despite extensive reforestation over the past century, many secondary forest sites that are environmentally suitable for mesophytic rich cove vegetation do not support the suite of species typical of these communities, apparently because of the dispersal limitations of forest herbs, particularly those with insect-dispersed seed and those with no morphological adaptations for long-distance seed dispersal. Harrelson and Matlack (2006) concurred with Bellemare (2002), even though abundance was much higher in their abandoned pastures (young stands) compared to the old stands (Table 1), young stands were compositionally distinct from old stands.

Conversion of temperate forest to agriculture alters soil physical, chemical, and microbial properties, which may influence subsequent reforestation (Flinn and Vellend 2005, Dyer 2010, Gilliam and Dick 2010). Factors that seem to influence recolonization include seed production, germination requirements, seedling herbivory, and especially seed dispersal ability. Species under-represented in secondary forests are often dispersed by gravity (barochory), ballistically (explosive; autochory) or by ants (myrmecochory), although Mitchell et al. (2002) concluded that historic land use alone did not necessarily limit ant dispersal. They found that the interactions among historic land use, patch size, and diversity and composition of ant species was complex. For example, small patches with high past disturbance had a reduced abundance of myrmecochorous plant species, even though these same environments supported a high abundance and diversity of ant species. Their data suggested that a shift in the ant community from one dominated by *Aphaenogaster* to one co-dominated by *Aphaenogaster* and *Camponotus* could have negative consequences for myrmecochores, because the *Camponotus* often consume the entire seed. If seeds are not eaten, post-germination seedling survivorship is at risk by harsh surroundings since seeds are transported by the *Camponotus* to their nests in logs and stumps that experience desiccation during periods of low precipitation. In contrast, *Aphaenogaster* ants consume only the elaiosome and transport seeds a shorter distance (Mitchell et al. 2002). Thus, the loss of *Aphaenogaster* species in small forest patches may be related to the loss of plant diversity.

OTHER STRESSORS. Additional factors other than logging and agriculture can be detrimental to forest herbs, including chronic deer herbivory (Griggs et al. 2006, Krueger and Peterson 2009, Leege et al. 2010, Royo et al. 2010, Aronson and Handel 2011), wind disturbance (Krueger and Peterson 2009), invasive species (Miller and Gorchov 2004, Griggs et al. 2006, Chapman et al. 2012), harvesting of herbs (Small et al. 2011), atmospheric pollutants (Matyssek et al. 2012), and climate change (Bullock 2012). Following intensified deer harvests, Royo et al. (2010) observed a moderate recovery of the herbaceous community. Abundance, height, and flowering of *Trillium* spp., cover of *Maianthemum canadense* Desf., and height of *Medeola virginiana* L. all increased following deer-herd reductions (Krueger and Peterson 2009). Slash abundance and fern cover following windthrow have been shown to reduce herb richness and diversity (Krueger and Peterson 2009); however, we found that windthrow followed by salvage logging increased herb richness and diversity due to disturbance of slash and microsite topography (see below, Elliott et al. 2002).

Old-growth forests are typically thought to be resistant to invasive species, with most non-native species penetrating less than 30 m into the forest interior (Hanu and Gibson 2008). The majorities of exotic, invasive plant species are shade-intolerant and are mostly fast-growing species (e.g., Hartman and McCarthy 2008). Shade-tolerant exotics are less abundant: however, more evidence is amassing about these species invading forest interiors (see Martin et al. 2009). For example, Chapman et al. (2012) found invasive species such as *Ailanthus altissima* (Mill.) Swingle, *Rosa multiflora* Thunb., *Microstegium vimineum* (Trin.) A. Camus, and *Paulownia tomentosa* (Thunb.) Siebold & Zucc. ex Steud. within the interior of an old-growth forest in eastern Kentucky. Martin et al. (2009) listed 139 exotic species considered capable of invading deeply shaded forest interiors. Considerable research and monitoring has been conducted on *Microstegium vimineum* (Gibson et al. 2002, Flory and Clay 2010, Schramm and Ehrenfeld 2010, Fraterrigo et al. 2011, Huebner 2011), *Alliaria petiolata* (M. Bieb.) Cavara & Grande (Rodgers et al. 2008), and *Celastris orbiculatus* Thunb. (McNab and Loftis 2002), but most exotic species have received much less attention.

Invasive pests such as hemlock woolly adelgid (HWA, *Adelges tsugae* Annand), elongate hemlock scale (*Fiorinia externa* Ferris), emerald ash borer (*Agrilus planipennis* Fairemaire), gypsy moth (*Lymantria dispar* L.), and the pathogen *Phytophthora ramorum* are known to infest and infect forest trees, resulting in growth reduction and mortality. Numerous studies have been conducted on the influence of these pests and pathogens on their associated host trees (for reviews see: Coyle et al. 2005, Lovett et al. 2006), but little information is available on how invasive species influence native forest herbs (Ford et al. 2012, Kapfl et al. 2012, Martin and Goebel 2013). Kapfl et al. (2012) described changes in the overstory of *Tsuga canadensis* forests with five to six years of HWA infestation, but little change in the understory composition. They attributed this lack of understory response to the co-occurrence of *Rhododendron maximum*, a dominant ericaceous shrub in many of their sample plots. Ford et al. (2012) found recruitment and growth of herbs and tree seedlings only in the interspaces between *R. maximum* patches within canopy gaps created by *T. canadensis* mortality.

Rich coves of central and southern Appalachian forests are sources of medicinal and edible plants, including such prominent species as *Panax quinquefolius* L. (American ginseng), *Hydrastis canadensis* L. (goldenseal), *Allium tricoccum* Aiton (ramps) and *Actaea racemosa* (black cohosh) (Chamberlain et al. 2002). Despite their importance and prominence, relatively few studies have examined harvest impacts on native Appalachian forest herbs, and those that have been conducted show pronounced impacts on natural populations (Van der Voort et al. 2003, Rock et al. 2004, Sanders and McGraw 2005, Albrecht and McCarthy 2007).

Ozone sensitivity has been documented for some woody species (Matyssek et al. 2012), but little is known about the ozone sensitivity of forest herbs. Acidic deposition of sulfate and nitrate can reduce growth of tree species (Matyssek et al. 2012) and interact with other stressors resulting in mortality. This is particularly well documented for *Picea rubens* Sarg. (Lawrence et al. 2012). Acidic deposition may be of specific concern in mesophytic rich coves because deposition of sulfate and nitrate is known to displace cations (Ca, Mg, and K) from forest soils (Federer et al. 1989, Gilliam et al. 2006, Elliott et al. 2008).

Future warmer temperatures are predicted to increase rates of tree mortality (Allen and Breshears 2007, IPCC 2007), and also to result in vegetation die-off events through an exacerbation of metabolic stress associated with drought (Adams et al. 2009). In a recent review, Allen et al. (2010) documented recent cases of increased tree mortality and die-offs triggered by drought and/or high temperatures, suggesting that amplified forest mortality may already be occurring in response to climate change. Compared to woody species, forest herbs may be even more sensitive to drought and heat stress and less likely to track the velocity of climate change due to limited dispersal distances (Bullock 2012). For example, in the Pacific Northwest, where mean temperature has increased by 2 °C since 1948, Harrison et al. (2010) found multiple herb-community changes consistent with an effectively drier climate, including lower relative cover by species of northern biogeographic affinity, and greater compositional resemblance to communities in southerly topographic positions. Changes in phenology (flowering and fruiting time) with rising temperatures and latitudes have been documented for some forest herbs (Warren et al. 2011), while other species were not as sensitive (De Freene et al. 2009). Climate change may also alter dispersal distance of some plants directly by changing the behavior of dispersal vectors (e.g., birds, mammals) or selection for increased dispersal ability (i.e., evolutionary processes; Bullock 2012).

DO ENVIRONMENTAL FACTORS EXPLAIN HERB SPECIES RICHNESS MORE THAN TIME SINCE DISTURBANCE? Fine-scale heterogeneity of species richness is an important component of community structure that ecologists have been trying to model for quite some time, with variable results. In a widely cited review on factors explaining local-scale plant (mostly herbaceous) species richness, Grace (1999) reported that ca. 57% (range: 23%–89%) of the variance of richness could be explained by various environmental factors, such as plant biomass, resources, abiotic conditions, disturbances, and soil microbial effects. In another study, Houle (2007) found a statistically significant model to explain herbaceous species richness using soil pH, elevation, and tree basal area; however, only 10% of the variation was explained. In a mature *Acer/Fagus* forest, Welch et al. (2007) showed that herbaceous-layer species were distributed across a gradient of soil pH, soil available phosphorus, and base cations, and their model explained 42% of the variation with the first two canonical axes.

Ulrey (2002) identified indicator species of rich cove forests based on 188 0.1-ha plots sampled across the southern Appalachians (Table 3), and he delineated five associations: Typic, High elevation-North, Nutrient-rich, Red Oak, and High elevation-South. The associations demonstrate the range of variation that can be expected for rich cove forests. Of these five associations, the Nutrient-Rich and Red Oak forests had significantly higher species richness than the other three. There were also significant differences in environmental variables such as precipitation and soil pH, calcium availability, and cation exchange capacity among associations. Similarly, from 2,475 0.1-ha plots sampled across western North Carolina, Simon et al. (2005) mapped 601 plots as rich cove forests based on their environmental characteristics. They concluded that the indicator species of those rich-cove forests were: *Cimicifuga racemosa*, *Panax quinquefolius*, *Caulophyllum thalictroides* (L.) Michx., *Sanguinaria canadensis* L., *Adiantum pedatum* L., *Aristolochia macrophylla* Lam., *Disporum lanuginosum*, *Botrychium virginianum* (L.) Sw., *Osmorhiza claytonii*, *Tilia americana* var. *heterophylla* (Vent.) Loudon, *Fraxinus americana*, *Liriodendron tulipifera*, *Quercus rubra*, and *Aesculus flava*.

ARE SPECIES UNIQUE TO OLD OR UNLOGGED FORESTS? Bunn et al. (2010) recently described plant species within Great Smoky Mountains National Park (GSMNP). They listed 50 herbaceous species that were found only in a forest stand with no history of logging (Table 4) and not found in a nearby stand that was logged in the 1920s. We compared this list of 50 species to data from the Coweeta Basin, an area that was also heavily logged in the 1920s (Table 4). Only 12 of the 50 species in the GSMNP unlogged area were not found within the Coweeta Basin, whereas the remaining 38 species (76%) are present, sometimes frequently, in logged forest stands at the Coweeta Basin. The 12 species not found included *Achillea millefolium* L. var. *occidentalis* DC., *Cardamine concatenata* (Michx.) Sw., *Chrysosplenium americanum* Schwein. ex Hook., *Cheilanthes* sp., *Circaea alpina* L., *Cystopteris protrusa* (Weath.) Blasdell, *Hydrophyllum virginianum* L. var. *atranthum* (Alexander), *Smilax tamnoides* L., *Stachys clingmanii* Small, *Thalictrum pubescens* Pursh, *Thaspium trifoliatum* (L.) A. Gray, *Veratrum viride* Aiton (Table 4). Because *Carex* and *Dichanthelium* species have not been fully identified to species level in the Coweeta Basin, we cannot be certain that *Carex digitalis* and *Dichanthelium boscii* (Poir.) Gould & C.A. Clark are not present within the Basin. Jackson et al. (2009) also found rich cove indicator species (Ulrey 2002, Table 3) in stands logged in the 1920s and in stands with no logging history. They reported only eight species with greater abundance in unlogged stands compared to logged stands. In general, species richness (S) was similar between mature secondary and old-growth stands, both age classes contained a high number of rich cove species, and no herb species was unique to old growth stands only. Collectively, the results of the reviewed studies reinforce our conclusion that factors controlling herbaceous species presence and abundance are highly complex, and that broad generalizations about the impacts of a single factor (e.g., logging) should be interpreted with caution.

PLANT DEMOGRAPHIC INFLUENCES ON RICH COVES. Regardless of environmental suitability, plant demography can limit the sustainability and recovery of rich cove forests after disturbance. Seed production, seed dispersal (mode and distance), seed germination,

Table 3. Herbaceous species that are indicators of rich cove forests of the southern Appalachians (based on Ulrey 2002).

Species	
Scientific name	Common name
Adiantum pedatum	Maiden-hair fern
Ageratina altissima	White snakeroot
Arisaema triphyllum	Jack-in-the-pulpit
Aster divaricatus [Eurybia divaricata]	White wood aster
Athyrium asplenoides [A. felix-femina]	Lady-fern
Botrychium virginianum	Rattlesnake fern
Caulophyllum thalictroides	Blue cohosh
Cimicifuga racemosa	Black cohosh
Collinsonia canadensis	Richweed
Deparia acrostichoides	Silver false spleenwort
Dioscorea quaternata [D. villosa]	Wild yam
Disporum lanuginosum [Prosartes lanuginosum]	Mandarin/Fairy-bells
Dryopteris intermedia	Fancy wood-fern
Dryopteris marginalis	Marginal wood-fern
Galium triflorum	Sweet scented bedstraw
Goodyera pubescens	Downy rattlesnake plantain
Hydrophyllum canadense and *H. virginianum*	Eastern waterleaf
Impatiens capensis	Orange jewel-weed
Laportea canadensis	Canadian woodnettle
Medeola virginiana	Cucumber root
Osmorhiza claytonii	Sweet cicely
Panax quinquefolius	Ginseng
Polygonatum biflorum	Solomon's seal
Polystichum acrostichoides	Christmas fern
Prenanthes sp.	Rattlesnake-root
Sanguinaria canadensis	Bloodroot
Smilacina racemosa [Maianthemum racemosum]	False Solomon's seal
Solidago curtisii	Goldenrod
Thelypteris noveboracensis	New York fern
Tiarella cordifolia	Foamflower
Trillum erectum	Purple trillium
Viola canadensis	Tall white violet
Viola rotundifolia	Round leaved yellow violet
Viola sp.	Violet sp.

seedling survival, and seedling growth are life history stages that can influence recruitment and colonization by forest herbs. All these life history stages are important in determining the longevity of a woodland herb in a particular forest environment. While seed bank and rhizome integrity may contribute to the recovery of forest herbs if the disturbance is not too severe, the most important factor affecting recruitment into a disturbed site is seed dispersal distance. Seed dispersal and flowering phenology have been shown to be important factors in recovery of forest herbs in restoration sites (McLachlan and Bazely 2001). Mode of dispersal is highly related to dispersal distance (Chambers and MacMahon 1994, Zelikova et al. 2008). For example, seeds dispersed by ants (myremechores) are moved a much shorter distance than those dispersed by wind (anemochores). Spatial patterns of seed dispersal are usually shown as negative exponential curves, where the number of seeds dispersed declines as the distance from the parent plant increases. The tail of these dispersal curves represents long-distance dispersal events that are, by definition, uncommon.

Ant-plant mutualisms represent one of the most common modes of seed dispersal among woodland herbs (Beattie 1985, Gaddy 1986). Approximately 50% of the rich cove herbs in the southern Appalachians are myrmecochores (Sorrels and Warren 2011). Although the transport of seeds by ants may provide plants with increased opportunities for germination, ants rarely move seeds more than a few meters (Beattie and Hughes 2002); hence, ant dispersal is strictly local-scale. Sorrels and Warren (2011) examined the correspondence between forest stand age and the abundance of an ant-dispersed herb, *Hexastylis arifolia*

(Michx.) Small, and a wind-dispersed herb, *Goodyera pubescens* (Willd.) R. Br. Vegetation was sampled in various-aged forest stands in the Bent Creek Experimental Forest in the southern Appalachian Mountains. Variance in *H. arifolia* and *G. pubescens* presence and abundance was assessed as a function of tree age and density. Both plant species were absent from plots where trees were < 20 years old, but only the ant-dispersed *H. arifolia* did not occur in stands < 34 years old.

Woodland herbs often grow clonally, have little recruitment by seed, and possess no obvious mechanism for long-distance dispersal (Bierzychudek 1982). Some studies have examined recruitment of clonal species such as *Arisaema triphyllum* (L.) Schott (Bierzychudek 1982, Levine and Feller 2004), *Trillium recurvatum* Beck (Sawyer 2010, Moore et al. 2012), *Trillium reliquum* J.D. Freeman (Gonzales and Hamrick 2005), and other non-clonal trilliums (Jules 1998, Webster and Jenkins 2008). Recruitment by seed can be limited in clonal herbs and highly variable in space and time. Some forest herbs such as *Uvularia perfoliata* have a ‘waiting’ strategy, in which vegetative ramet production maintains populations under a closed forest canopy while seed production is stimulated in canopy gaps (Kudoh et al. 1999). Rhizome traits of clonal colonies may differ among perennial forest herbs in terms of rhizome thickness, rooting depth, and rate of spread. For example, *Podophyllum peltatum* L. has extensive rhizogenous systems that allow it to spread and survive as large established colonies (Lata et al. 2002).

Clonal herbs that attain maturity in late-seral forests are often assumed to have similar responses to disturbance and to be functionally equivalent. However, variation among clonal herbs in demographic and physiological response to disturbance has also been shown. For example, Nelson et al. (2007) assessed demographic changes and physiological acclimation of three clonal herbs (*Asarum caudatum* Lindl., *Clintonia uniflora* (Menzies ex Schult. & Schult. f.) Kunth, and *Pyrola picta* Sm.) that differ in belowground morphology and leaf longevity following harvest of a mature coniferous forest. They demonstrated that forest herbs with greater rhizome plasticity (i.e., depth and horizontal spread) and shorter leaf duration have greater potential to acclimate after disturbance than those with rigid architectures and persistent leaves. Thus, species with comparable successional roles can vary substantially in their demographic and physiological responses to disturbance, with potential consequences for long-term recovery.

Ability of shade-tolerant species to store seeds in the soil (i.e., seed bank) could be a mechanism to recover rapidly from disturbance. Hall et al. (2010) found 12 species in the seed bank of topsoil that was relocated before mining, including some forest herbs such as a *Desmodium* sp., *Maianthemum (Smilacena) racemosum*, and *Polygonatum biflorum* (Walter) Elliott. In southeastern Ohio, Small and McCarthy (2010) found poor representation of herb species in the seed bank, with a few shade-adapted (= “late-seral”) herb species and only a slightly greater number of early-seral herbs (e.g., *Erechtites hieraciifolia, Solanum nigrum* L., *Eupatorium serotinum* Michx., and *Phytolacca americana*) regardless of stand age. Hawkins et al. (2007) studied the seed biology of six eastern forest herbs in the Apiaceae. They found that regardless of seed mass and morphology, germination of only a few seeds of *Cryptotaenia canadensis* (L.) DC., *Osmorhiza claytonii*, and *Sanicula gregaria* E.P. Bicknell occurred and was delayed until the fourth year after sowing. In this study as well, germination of a few seeds of *S. canadensis* L., *S. trifoliata* E.P. Bicknell, and *Thaspium barbinode* (Michx.) Nutt. did not occur until the sixth year, demonstrating that at least some forest herbs have a limited potential to form a seed bank. Whigham et al. (2006) investigated the seed viability of seven terrestrial orchids, and they found species-specific differences in seed viability and *in situ* seed germination rates. For example, most *Goodyera pubescens* seeds germinated within one year (no seed bank), while *Platanthera lacera* (Michx.) G. Don and *Galearis spectabilis* (L.) Raf. formed seed banks that lasted for three years, and four other species formed a seed bank that lasted from 4–5 (*Corallorhiza trifida* Chatelain) to almost 7 years (*Aplectrum hyemale* (Muhl. ex Willd.) Torr., *Liparis liliifolia* (L.) Rich. ex Ker Gawl., *Tipularia discolor* (Pursh) Nutt.).

MESOPHYTIC RICH COVES IN THE COWEETA BASIN. We examined original data from seven watersheds within the Coweeta Basin (Table 2) in order to evaluate species diversity and composition and determine which species are more prevalent in unmanaged forests than in

Table 4. Comparison of species found only in unlogged areas of the GSMNP (Bunn et al. 2010) and presence of those species in the Coweeta Basin, logged between 1900 and 1923. Species present (√) or absent (–) within the Coweeta Basin.

Species		
Scientific name	Common name	Present (√)
Thaspium trifoliatum	Purple meadowparsnip	–
(*Thaspium barbinode* (Michx.) Nutt.)	Hairyjoint meadowparsnip	√
Achillea millefolium var. *occidentalis*	Western yarrow	–
(*Achillea millefolium* L.)	Common yarrow	√
Symphyotrichum acuminata [*Aster acuminatus* Michaux.]	-	√
Symphyotrichum lateriflorum var. *lateriflorum* [*Aster lateriflorus* (L.) Britt.]	Calico aster	√
Symphyotrichum undulatum [*Aster undulatus* L.]	Wavy leaf aster	√
Cardamine concatenata	Cutleaf toothwort	–
(*Cardamine diphylla*, *C. clematitis*, *C. hirsuta*)	-	√
Clethra acuminata	Mountain pepperbush	√
Carex digitalis	Slender woodland sedge	–
(*Carex* spp.)	-	√
Dennstaedtia punctilobula	Eastern hayscented fern	√
Cystopteris protrusa	Lowland bladderfern	–
Vaccinium pallidum	Blue Ridge blueberry	√
Vaccinium stamineum	Deerberry	√
Gentiana decora	Showy gentian	√
Hydrophyllum virginianum var. *atranthum*	Appalachian waterleaf	–
(*Hydrophyllum canadense* and *H. virginianum* L.)	Eastern waterleaf	√
Iris cristata	Dwarf crested iris	√
Collinsonia canadensis	Richweed	√
Monarda clinopodia	Lemon-mint, white bergamot	√
Stachys clingmanii	Clingman's hedgenettle	–
(*Stachys latidens* Small and *S. tenuifolia* Willd.)	-	√
Lilium superbum	Turk's cap lily	√
Melanthium parviflorum [*Veratrum parviflorum* Michx.]	Appalachian bunchflower, small-flowered false hellebore	√
Polygonatum pubescens	Hairy Solomon's seal	√
Streptopus roseus	Twistedstalk	√
Uvularia grandiflora	Largeflower bellwort	√
Uvularia perfoliata	Perfoliate bellwort	√
Veratrum viride	Green false hellebore	–
Monotropa uniflora	Indianpipe	√
Circaea alpina	Small enchanter's nightshade	–
Circaea lutetiana ssp. canadensis	Broadleaf enchanter's nightshade	√
Galearis spectabilis [*Orchis spectabilis* L.]	Showy orchid	√
Osmunda cinnamomea	Cinnamon fern	√
Dichanthelium boscii	Bosc's panicgrass	–
(*Dichanthelium spp.*)	Panicgrass	√
Adiantum pedatum	Maidenhair fern	√
Cheilanthes sp.	Lipfern	–
Chimaphila maculata	Spotted wintergreen	√
Ranunculus recurvatus	Blisterwort, buttercup	√
Thalictrum clavatum	Mountain meadow-rue	√
Thalictrum dioicum	Early meadow-rue	√
Thalictrum pubescens	King of the meadow	–
Trautvetteria caroliniensis	Carolina bugbane	√
Aruncus dioicus	Bride's feathers	√
Porteranthus trifoliatus	Bowman's root	√
Potentilla simplex	Common cinquefoil	√
Chrysosplenium americanum	American golden saxifrage	–
Viola pedata	Birdfoot violet	√
Smilax tamnoides [*Smilax hispida* Muhl. ex Torr.]	Bristly greenbrier	–

managed forests. Three were reference watersheds, while the others had been subjected to varying degrees of disturbance. Many mesophytic rich cove indicator species (Ulrey 2002, Simon et al. 2005) were found in each of the Coweeta watersheds regardless of disturbance history (Table 6). However, partially disturbed sites (WS28 and WS34) and reference sites

(WS34, WS14, and Reynolds) had more indicator species than clearcut sites (WS6, WS7, and WS13) (Table 6). Five rich cove indicator species occurred in all watersheds, otherwise there was variation among watersheds in terms of which species were present. *Osmorhiza claytonii*, listed as a rich cove species by Ulrey (2002), was not observed within the Coweeta Basin (Pittillo and Lee 1984). Each watershed exhibited a long-tailed, negative exponential, dominance-diversity curve with a few species dominating. Total number of herb species ranged from 37 to 61, but fewer than ten species accounted for 57–90% of the total herbaceous cover (Appendix A). The species identity that contributed to the top ten varied across the seven watersheds.

All three clearcut watersheds were comparable in terms of S and H′, but WS6 was dominated by one early-seral species (*Eupatorium rugosum* Houtt.) and had fewer indicator species than WS7 or WS13. WS6, the most severely disturbed site, had the least number of indicator species (15 of 38, Table 6), and only five of these were relatively abundant (*P. acrostichoides*, *D. punctilobula* (Michx.) T. Moore, *A. pedatum*, *D. nudiflorum* (L.) DC., and *T. cordifolia*). Even after canopy closure and 28 years since disturbance, *E. rugosum*, remained the most abundant (Appendix A). Considering the intense disturbance that occurred over an 11-yr period, (i.e., cutting, burning, soil scarification, planting to grass, fertilization, liming, and herbicide (Table 2), it is remarkable that any indicator species herbs have colonized WS6 as rapidly as a few decades. It is likely that the soil scarification and grass competition deteriorated the rhizomes of clonal species and the herb species' seed bank (Elliott et al. 1998). Thus, seed dispersal was probably the only mode of recruitment into WS6. Myrmecochore plants were lacking in this watershed, with the exception of *T. cordifolia*; whereas, wind-dispersed ferns were more abundant.

WS7, a low elevation, south-facing watershed, was sampled immediately after clearcut in 1977 and re-sampled 30 years later (Table 2). A small portion (15%) of the watershed contains a rich cove community where several indicator species such as *Thelypteris noveboracensis* (L.) Nieuwl., *Arisaema triphyllum*, *Viola* spp., and *Polygonatum biflorum* were relatively abundant (Table 6). Surprisingly, myrmecochore plants were relatively abundant, possibly because cutting alone did not reduce ant populations. Herbaceous-layer S and H′ have increased with time since disturbance (Table 2), but herb species H′ remains lower than reference watersheds (Table 5).

WS13, a low elevation watershed, was clearcut twice in the last century, and consequently is dominated by *L. tulipifera* trees in the overstory (Table 2). The herbaceous layer was measured once in 1991. More than half of the total herb species present were rich cove indicator species, including ten myrmecochore plants (Table 6). The most abundant species were *Polystichum acrostichoides*, *Viola rotundifolia* Michx., *Athyrium felix-femina* (L.) Roth, *Arisaema triphyllum*, *Galium latifolium* Michx., and *Thelypteris noveboracensis* (Appendix A).

WS28 is a high elevation watershed where the mesophytic cove was thinned in 1963 to favor *L. tulipifera* trees (Table 2). The herbaceous-layer was sampled 28 years after the thinning treatment (Parr 1992). Species richness and diversity were higher in WS28 than more recently disturbed watersheds in the Coweeta Basin (Table 5). Of the 41 herbaceous species recorded in WS28, 27 were species (Table 6) which are considered indicators of rich mesophytic coves (Ulrey 2002, Simon et al. 2005). The most abundant species were *Thelypteris noveboracensis*, *Laportea canadensis*, and *Viola* spp.

WS34, a high elevation watershed, was heavily damaged by Hurricane Opal in 1995 (Table 2). Following the blowdown of trees, approximately 10 ha were salvage logged in 1996. Elliott et al. (2002) compared the hurricane-then-salvage-logged (H+S) area to an undisturbed reference area within WS34. Abundance of herbaceous-layer species was higher in the H+S forest than in the undisturbed forest, and herbaceous-layer abundance increased over time in the H+S forest. More species were represented by the various growth forms (trees, shrubs, vines, and herbs) in the H+S than in the undisturbed forest. More species were represented by indicator species (or shade-adapted) and early-seral (shade-intolerant) categories in the H+S forest than in the undisturbed forest. In addition, some indicator species that were found in both forests were more abundant in the H+S forest; these included *Arisaema triphyllum*, *Cimicifuga racemosa*, *Galium lanceolatum* Torr., *Oxalis stricta* L., *and Viola* spp. (Appendix A). Not

Table 5. Herb species richness (S_{herbs}), diversity (H'_{herbs}), and evenness (E_{herbs}) and herbaceous-layer richness ($S_{herbs+woody}$), diversity ($H'_{herbs+woody}$), and evenness ($E_{herbs+woody}$) in mesophytic coves of seven watersheds in the Coweeta Basin*. Standard errors are in parentheses.

Watershed	S_{herbs}	H'_{herbs}	E_{herbs}	$S_{herbs+woody}$	$H'_{herbs+woody}$	$E_{herbs+woody}$
WS28, partial cut	30.4 a	2.151 a	0.579	–	–	–
	(2.2)	(0.079)	(0.021)			
WS34, partial cut	23.1 b	2.404 a	0.768	33.5	2.701	0.773
	(1.7)	(0.149)	(0.034)	(1.9)	(0.087)	(0.019)
WS7, clearcut	6.8 d	1.135 c	0.646	10.4	1.440	0.610
	(1.0)	(0.158)	(0.072)	(1.2)	(0.198)	(0.069)
WS13, clearcut	7.3 d	1.376 c	0.771	11.1	1.780	0.797
	(1.0)	(0.168)	(0.030)	(1.5)	(0.154)	(0.025)
WS6, clearcut	8.8 d	1.124 c	0.520	12.1	1.727	0.579
	(0.4)	(0.091)	(0.038)	(0.7)	(0.077)	(0.029)
WS34, reference	15.5 c	1.980 ab	0.764	24.0	2.302	0.727
	(3.5)	(0.280)	(0.044)	(3.8)	(0.271)	(0.058)
WS14, reference	9.9 cd	1.556 b	0.760	13.3	1.660	0.700
	(1.7)	(0.157)	(0.032)	(1.9)	(0.150)	(0.040)
Reynolds, reference	16.2 c	1.827 b	0.657	22.5	2.167	0.699
	(0.9)	(0.112)	(0.034)	(1.2)	(0.110)	(0.030)

* Watershed descriptions are provided in Table 1. Individual species abundance in each watershed is provided in Appendix A. Values followed by different letters are significantly different ($\alpha = 0.05$) based on the Ryan-Einot-Gabriel-Welsch multiple range test in PROC GLM, SAS 9.3 (SAS Institute, Cary, NC, USA).

only were S and H′ higher in the H+S forest than in the undisturbed forest, genera richness and family richness were also higher (Elliott et al. 2002).

The H+S forest within WS34 had a large amount of slash left from logging, and pit-and-mound topography was created from the blowdown of large trees (Table 2). Following the 1995 hurricane event, Clinton and Baker (1999) measured considerable variation in soil characteristics (carbon, nitrogen, and C:N ratio), light (PAR; photosynthetically active radiation), soil moisture, and soil temperature within pit and mound microsites created by treefalls across the Coweeta Basin. The microtopography from uprooting of windthrown trees (Peterson and Campbell 1993, Foster et al. 1997, Beatty 2003), shade from the slash-debris left on site after the salvage logging, and shade from the remaining overstory trees created a mosaic of environmental conditions. Thus, the environmental heterogeneity in partially disturbed sites can support a mix of early-seral and shade-adapted (= "late-seral") herbaceous species, and a corresponding higher species richness and diversity than a clearcut or abandoned agriculture site and possibly even an undisturbed forest (Elliott et al. 2002).

The Reynolds reference area is located in the center of Coweeta Basin (Table 2), near a perennial stream (Reynolds Branch), and a study was established to characterize the functional diversity of its mesophytic rich coves. Prior to treatments, the herbaceous-layer was surveyed in 1998. Reynolds reference had the highest H′ of herb species among the low elevation watersheds (WS6, WS7, and WS13), and it had the highest number of indicator species of all watersheds (Tables 6). *Thelypteris noveboracensis* was the most abundant species with nearly 50% relative cover, followed by *Tiarella cordifolia*, *Viola* spp., *T. hexagonoptera* (Michx.) Weath., and *Thalictrum dioicum* L. (Appendix A).

Results from the Coweeta watersheds concur with other studies (Jenkins and Parker 2000, Elliott and Knoepp 2005, Ristau et al. 2011, Zenner et al. 2012), indicating that partial cutting does not reduce herb species diversity and that many shade-adapted herbs are maintained. Review of the literature showed that most studies reported only 'herbaceous-layer' S and H′ (Table 1). Because such data include woody species, there is uncertainty about the contribution of forest herbs to overall diversity. For example, in Coweeta watersheds, woody species comprised between 26 to 37% of the total number of species in the herbaceous layer (Appendix A); consequently, herb species S and H′ were much lower than 'herbaceous-layer' (herbs + woody species) S and H′ (Table 5). Only with the original data sets could one disentangle 'forest herbs' from 'herbaceous-layer' reporting of diversity. Indices of diversity (S, H′, and

Table 6. Herbaceous species indicator list for mesophytic rich coves (based on Ulrey 2002) within the Coweeta Basin. Species present (√) or absent (–) in eight watersheds with different disturbance histories. The watersheds are: WS6, grass-to-forest succession (28-yr-old); WS7, cable-logged clearcut 1977 (30-yr-old); WS13 coppice clearcut 1939 and 1962 (30-yr-old); WS28, thinned 1963 (28-yr-old); WS34, wind then salvage-logged 1995–96 plus WS34, undamaged reference; WS14, reference; and Reynolds, reference. All reference areas are mature 70+ yr-old forests, unmanaged since 1923.

Species	WS 6	WS 7	WS 13	WS 28	WS 34	WS34 reference	WS14 reference	Reynolds reference
Actaea pachypoda	–	√	–	√	–	–	–	√
Adiantum pedatum	√	–	√	–	–	–	–	√
*Anemone quinquefolia**	√	–	–	–	√	–	–	√
Arisaema triphyllum	√	√	√	√	√	√	√	√
Aster divaricatus	√	√	√	√	√	√	√	√
Athyrium felix-femina	–	√	–	√	–	–	√	√
Botrychium virginianum	√	–	√	√	√	–	–	√
Caradamine diphylla	√	–	–	–	–	–	√	√
Caulophyllum thalictroides	–	–	–	√	√	–	–	√
Cimicifuga racemosa	–	–	–	–	√	√	√	√
Collinsonia canadensis	–	√	–	√	–	–	√	√
Dennstaedtia punctilobula	√	–	–	–	–	√	√	√
Desmodium nudiflorum	√	√	√	√	√	√	√	√
Dioscorea villosa/quaternata	√	–	√	√	√	√	√	√
*Disporum lanuginosum**	–	–	–	–	√	–	√	√
Dryopteris spp. (*intermedia*, *marginalis*)	√	–	–	–	√	√	√	√
*Erythronum americanum**	?	?	?	√	?	?	√	√
Galium spp. (*circaezans*, *latifolium*, *lanceolatum*)	–	–	√	√	√	√	√	√
Gentiana spp. (*decora*, *quinquefolia*, *saponaria*)	–	–	–	√	√	–	–	√
Laportia canadensis	–	–	–	√	–	–	–	–
*Lysimachia quadrifolia**	–	–	√	–	√	√	√	√
*Medeola virginiana**	–	–	√	√	√	–	√	√
Monarda clinopodia	–	√	√	√	√	–	–	√
*Orchis spectabilis**	–	√	√	√	–	–	–	√
Osmorhiza claytonii	–	–	–	–	–	–	–	–
Osmunda cinnamomea	√	–	√	–	–	–	√	√
Panax quinquefolius	–	–	–	√	–	–	√	√
*Polygonatum biflorum**	–	√	√	√	√	√	√	√
Polystichum acrostichoides	√	√	√	√	√	√	√	√
Prenanthes spp.	√	√	√	√	√	√	√	√
*Sanguinaria canadensis**	√	√	√	–	√	√	–	√
Solidago curtisii	√	√	√	√	√	√	√	√
*Smilacina racemosa**	–	√	√	–	√	√	√	–
Thalictrum spp. (*dioicum*, *thalictroides*, *clavatum*)*	√	–	√	√	√	√	√	√
Thelypteris noveboracensis	–	√	√	√	√	√	√	√
*Tiarella cordifolia**	√	√	√	√	–	–	√	√
Trillium spp. (*erectum*, *undulatum*, *catesbaei*)*	–	√	–	√	√	√	√	√
*Triphora trianthophora**	–	√	–	–	–	–	–	–
Uvularia spp. (*perfoliata*, *pudica*)*	–	–	√	√	√	√	√	√
*Veratrum parviflorum**	–	√	√	√	√	–	√	√
*Viola rotundifolia**	√	–	√	√	√	√	√	√
Viola spp. (*blanda*, *cucullata*, *canadensis*)*	√	√	√	√	√	√	√	√
Total no. of rich cove species	15	16	22	23	24	17	24	32
Total no. of herbaceous species	38	37	40	41	66	42	56	61

Note: * denotes myrmecochore species. *Erythronum americanum* has been observed in many rich cove forests across the Coweeta Basin (P. Clinton, personal observation); due to its early spring arrival and rapid senescence it is often not recorded in late spring-summer samples.

E) that incorporate species identity may be better measures of recovery in mesophytic rich coves, particularly where rich cove indicator species have been replaced by early-seral or woody species.

KNOWLEDGE GAPS. Collectively, the results of the reviewed studies reinforce our conclusion that factors controlling herbaceous species presence and abundance are highly complex, and that broad generalizations about the impacts of a single factor (e.g., logging) should be interpreted with caution. With this literature review and synthesis, we have identified several knowledge gaps in understanding mesophytic rich coves.

1) Diversity, disturbance and recovery.—A large pool of literature exists on disturbance and diversity (see Huston 1994, Gilliam and Roberts 2003, Gilliam 2007); however, this literature does not focus on the rate of recovery from disturbance events or the identity of the species contributing to the species pool. For example, diversity may increase following disturbances that open the canopy due to recruitment of early-seral species, such as those in the Asteraceae family, that are adapted to growth under high light conditions. In contrast, with some disturbance types early-seral and shade-adapted species may coexist for a period of time, at least until complete canopy closure has eliminated early-seral recruits. Identifying which shade-adapted species are indicators for 'high quality' rich cove forest would be a fruitful line of investigation.

   Indices such as S, H′, and E are quantitatively good estimates of diversity, because they incorporate species richness, relative abundance, and evenness of abundance. However, the way these indices are applied to assess diversity or recovery from disturbance may be inadequate or misleading, particularly for mesophytic rich coves. Incorporating all plant species (woody + herbaceous) below a height limit into a single index does not provide adequate information to evaluate the diversity and recovery of rich cove herbs. Furthermore, differentiating between indicator species (see Table 6) and early-seral herb species would provide additional information. For example, in WS28, indicator species comprised 56% of the total herb species present and 95% of the relative cover. In WS7, indicator species comprised 43% of the herb species present and 82% of the relative cover (Appendix A). Even though indicator species are recovering in WS7 after 30 years since clearcutting, the overall herb cover of WS7 is lower than the partially cut forest of WS28 (WS7, herb cover = 9.7%; WS28, herb cover = 36.2%). Little additional information is available to assess diversity and abundance of rich cove indicator species following disturbance.

2) Demography of forest herbs.—Few studies have examined the demography or physiology of forest herbs, particularly across all life stages (Whigham 2004). While some genera have been studied (e.g., *Hexastylis*, *Asarum*, *Trillium*, *Arisaema*, *Goodyera*, *Hepatica*, *Podophyllum*), little to no information exists for the majority of woodland herbs. Few studies are available on the soil seed bank of herbaceous species due to the difficulty of sampling and quantifying seeds (Hawkins et al. 2007) and even less is known about seed bank longevity. Species-specific life histories and the prevailing site conditions are important lines of research for understanding the recovery and sustainability of mesophytic rich cove forests.

3) Recovery of acidic coves.—Presence of evergreen species, particularly *Rhododendron maximum*, is an indicator of acidic coves in the southern Appalachians. Where acidic-coves and rich-coves (without *R. maximum* or *Tsuga canadensis*) are adjacent to one another, receive the same atmospheric deposition, and have the same parent material and similar physiography, one could assume that coves become acidic with low base cation conditions because ericaceous shrubs are present. Indeed, *R. maximum* produces long-lived, sclerophyllous leaves that are composed of lignin and tannins (and other polyphenols), which are highly recalcitrant (Monk et al. 1985). Its litter is slow to decompose and, thus, a thick recalcitrant litter layer develops under the *R. maximum* canopy where much of the nitrogen and cations in the humus layer are bound in complex organic compounds and are unavailable to non-ericaceous plants (Wurzberger and Hendricks 2007). Shifts in composition from evergreen to deciduous species may, over time, shift the recalcitrant litter pool to a more labile pool having high nutrient and low lignin contents in leaf tissue and decomposing relatively fast (Cornelissen et al. 2001). Whether herb species will recruit into formerly

acidic coves following shifts from evergreen to deciduous canopies is unknown.

4) Other stressors.—Little is known about how other stressors will affect rich cove species. Current and predicted climate change with increasing temperatures and variable and more extreme precipitation (Ford et al. 2011) may alter rich cove habitat. While forecasts of the future precipitation regime in the southern Appalachians are uncertain with respect to the mean (e.g., wetter vs. drier), an increasing variance is already clear, and is superimposed on rising mean annual temperature (Ford et al. 2011, Laseter et al. 2012). The intensification of summer drought conditions in some years will raise important ecological questions pertinent to rich cove herbs. Will the cool/moist microsites located in coves provide refuges for biodiversity as surrounding habitats become increasingly dry? Alternatively, are the rich cove species that dominate these highly diverse moist habitats vulnerable to drought (Clark et al. 2011, 2012)?

Conclusions and Management Considerations. Much of the available literature on herbaceous-layer response to disturbance is not specific to mesophytic rich coves; only eight of the 23 eastern deciduous forest papers highlighted in this review were specific to mesophytic coves (Table 1). An important outcome of our synthesis is that no single study or data set can provide conclusive evidence or clear management strategies; however, an overriding conclusion is that the magnitude of impact and the management actions necessary to restore herbaceous communities are directly proportional to the severity of disturbance, current condition, site heterogeneity, and historical land use. These factors, and with a host of others (e.g., climate variability, air pollution, and invasives) are likely to have a strong influence on the highly variable and inclusive patterns observed when comparing ‘old-growth’ or uncut forest herbaceous diversity to that of human disturbed forests. More specifically:

1) The first step for managing mesophytic coves in the southern Appalachians is to differentiate between rich coves and acidic coves. Acidic coves lack forest herbs because the ericaceous shrub midstory (*Rhododendron, Kalmia*) prevents colonization by forbs and grasses. If conversion of acidic coves to rich coves becomes a management objective, particularly with regards to the loss of *T. canadensis* forests due to HWA, removal of this shrub layer would be necessary before introducing an herbaceous flora. However, given the acidic soils beneath ericaceous shrubs, it may take years to decades before the acidity is neutralized enough for establishment of herb species adapted to higher soil pH and calcium.
2) Previous land-use history should be known and documented, to understand why abandoned agricultural lands may lack many of the species characteristic of rich coves (Bellemare et al. 2002). Major portions of eastern National Forests are comprised of abandoned agricultural land (Jenkins and Parker 2000, Singleton et al. 2001, Fraterrigo et al. 2009b, Thiemann et al. 2009). Forests on these lands often have reduced frequencies of many native forest herbs compared with forests that were never cleared for agriculture. A leading explanation for this pattern is that many forest herbs are dispersal-limited and the rhizosphere has been compromised (Fraterrigo et al. 2009b, Dyer 2010, Scott and Morgan 2012). Proximity to extant populations is a critical factor controlling the rate and timing of forest colonization, as seed rain decreases logarithmically with increasing distance from seed source (Harper 1977, Willson 1993). Thus, abandoned agricultural areas have a species composition that is highly variable and distinct from other disturbance types, and may require much more aggressive management activities (such as seeding or planting) to re-establish desired species.
3) Much attention has been given to logging as a driver of herb species S and H′ in forests (Jackson et al. 2009, Wyatt and Silman 2010); however, other stressors may be equally or even more important to consider in the future. Of the stressors known to affect forest trees such as native and invasive pests and pathogens, acidic deposition, air pollution, drought, and wind, little to no information exists on how these stressors affect herbaceous plants. Acidic deposition may be of

specific concern in mesophytic rich coves because deposited sulfate and nitrate are known to displace cations (Ca, Mg, and K) from forest soils (Federer et al. 1989, Elliott et al. 2008). Information on how forest herbs respond to acidic deposition is still lacking.

4) Climate change may have large impacts on mesic cove herbs. Models have demonstrated that climate change will gradually shift the locations of suitable habitats (IPCC 2007) and will likely influence mesophytic cove species in the southern Appalachians (Dale et al. 2010). Assisted migration (humans as dispersal vectors) has been heavily debated as a means for conservation (Vitt et al. 2009, Pedlar et al. 2012), particularly for tree species, and assisted migration for forest herbs may be equally as important.

5) Managing and sustaining mesophytic rich coves in the southern Appalachians requires knowledge of the environments (moisture, light, temperature, and nutrient availability) and autecology (species biology, demography, physiology, resource requirements and thresholds) of the herb species adapted to these forests. While much is known about a few species (Baskin et al. 1997, Hall et al. 2010), little is known about the preponderance of forest herbs that are indicators of rich coves (Table 3). Herb species richness and diversity are variable across environmental gradients, and the same suite of species cannot be expected to occur across this entire gradient. The rate of recovery of forest herbs from a disturbance not only depends on the disturbance severity, it also depends on the local environmental condition. Mesophytic rich coves, by definition, may recover more quickly than drier communities. For example, leaf area accumulation and canopy closure are more rapid in cove communities than in dry, mixed-oak communities; even within a few years after clearcutting, leaf area index can reach pre-disturbance levels, tempering environmental adversities caused by clearcutting (Elliott et al. 2002).

Literature Cited

ADAMS, H. D., M. GUARDIOLA-CLARAMONTE, G. A. BARRON-GAFFORD, J. C. VILLEGAS, D. D. BRESHEARS, C. B. ZOU, P. A. TROCH, AND T. E. HUXMAN. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proc. Nat. Acad. Sci. 106: 7063–7066.

ADLER, P. B., E. W. SEABLOOM, E. T. BORER, H. HILLEBRAND, Y. HAUTIER, A. HECTOR, W. S. HARPOLE, L. R. O'HALLORAN, J. B. GRACE, T. M. ANDERSON, J. D. BAKKER, L. A. BIEDERMAN, C. S. BROWN, Y. M. BUCKLEY, L. B. CALABRESE, C.-J. CHU, E. E. CLELAND, S. L. COLLINS, K. L. COTTINGHAM, M. J. CRAWLEY, E. I. DAMSCHEN, K. F. DAVIES, N. M. DECRAPPEO, P. A. FAY, J. FIRN, P. FRATER, E. I. GASARCH, D. S. GRUNER, N. HAGENAH, J. HILLE RIS LAMBERS, H. HUMPHRIES, V. L. JIN, A. D. KAY, K. P. KIRKMAN, J. A. KLEIN, J. M. H. KNOPS, K. J. LA PIERRE, J. G. LAMBRINOS, W. LI, A. S. MACDOUGALL, R. L. MCCULLEY, B. A. MELBOURNE, C. E. MITCHELL, J. L. MOORE, J. W. MORGAN, B. MORTENSEN, J. L. ORROCK, S. M. PROBER, D. A. PYKE, A. C. RISCH, M. SCHUETZ, M. D. SMITH, C. J. STEVENS, L. L. SULLIVAN, G. WANG, P. D. WRAGG, J. P. WRIGHT, AND L. H. YANG. 2001. Productivity is a poor predictor of plant species richness. Science 333: 1750–1752.

ALBRECHT, M. AND B. C. MCCARTHY. 2007. Comparative analysis of goldenseal (*Hydrastis canadensis* L.) population re-growth following human harvest: implications for conservation. Am. Midl. Nat. 156: 229–236.

ALBRECHT, M. A. AND B. C. MCCARTHY. 2009. Seedling establishment shapes the distribution of shade-adapted forest herbs across a topographical moisture gradient. J. Ecol. 97: 1037–1049.

ALLEN, C. D. AND D. D. BRESHEARS. 2007. Climate-induced forest dieback as an emergent global phenomenon. Eos. Trans. Am. Geophys. Union 88: 504.

ALLEN, C. D., A. K. MACALADY, H. CHENCHOUNI, D. BACHELET, N. MCDOWELL, M. VENNETIER, T. KITZBERGER, A. RIGLING, D. D. BRESHEARS, E. J. HOGG, P. GONZALEZ, R. FENSHAM, Z. ZHANGM, J. CASTRO, N. DEMIDOVA, J. -H. LIM, G. ALLARD, S. W. RUNNING, A. SEMERCI, AND N. COBB. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259: 660–684.

ARONSON, M. F. J. AND S. N. HANDEL. 2011. Deer and invasive plant species suppress forest herbaceous communities and canopy tree regeneration. Nat. Areas J. 31: 400–407.

BASKIN, J. M., K. M. SNYDER, J. L. WALCK, AND C. C. BASKIN. 1997. The comparative autecology of endemic, globally rare, and geographically wide-spread common plant species: three case studies. Southeastern Nat. 42: 384–399.

BEATTIE, A. J. 1985. The Evolutionary Ecology of Ant-Plant Mutualisms. Cambridge University Press, Cambridge, UK. 182 p.

BEATTIE, A. J. AND L. HUGHES. 2002. Ant-plant interactions, p. 211–235. *In* C. M. Herrera and O. Pellmyr [eds.], Plant-Animal Interactions: an Evolutionary Approach. Blackwell Science, Oxford, UK.

BEATTY, S. W. 2003. Habitat heterogeneity and maintenance of species in understory communities, p. 177–197. *In* F. R. Gilliam and M. R. Roberts [eds.], The Herbacous Layer in Forests of Eastern North America. Oxford University Press, New York, NY.

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.

BELOTE, R. T., N. J. SANDERS, AND R. H. JONES. 2009. Disturbance alters local–regional richness relationships in Appalachian forests. Ecology 90: 2940–2947.

BELOTE, R. T., R. H. JONES, AND T. F. WIEBOLDT. 2012. Compositional stability and diversity of vascular plant communities following logging disturbance in Appalachian forests. Ecol. Appl. 22: 502–516.

BIERZYCHUDEK, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecol. Monogr. 52: 336–351.

BULLOCK, J. M. 2012. Plant dispersal and the velocity of climate change, p. 366–377. *In* J. Clobert, M. Baguette, T. G. Benton, and J. M. Bullock [eds.], Dispersal Ecology and Evolution. Oxford University Press, Oxford, UK.

BUNN, W. A., M. A. JENKINS, C. B. BROWN, AND N. J. SANDERS. 2010. Change within and among forest communities: the influence of historic disturbance, environmental gradients, and community attributes. Ecography 33: 425–434.

CHAMBERS, J. C. AND J. A. MACMAHON. 1994. A day in the life of a seed: Movements and fates of seeds and their implication for natural and managed systems. Ann. Rev. Ecol. Syst. 25: 263–292.

CHAMBERLAIN, J. L., R. J. BUSH, A. L. HAMMETT, AND P. A. ARAMAN. 2002. Eastern national forests: managing for nontimber forest products. J. For. 100: 8–14.

CHANDY, S., Y. A. K. HONU, AND D. J. GIBSON. 2009. Temporal changes in species composition in permanent plots across the Shawnee National Forest, Illinois, USA. J. Torrey Bot. Soc. 136: 487–499.

CHAPMAN, J. I., K. L. PERRY, AND R. W. MCEWAN. 2012. Changing flora of an old-growth mesophytic forest: Previously undetected taxa and first appearance of non-native invasive species. J. Torrey Bot. Soc. 139: 206–210.

CLARK, J. S., D. M. BELL, M. H. HERSH, AND L. NICHOLS. 2011. Climate change vulnerability of forest biodiversity: climate and resource tracking of demographic rates. Global Change Biol. 17: 1834–1849.

CLARK, J. S., D. M. BELL, M. KWIT, A. POWELL, R. ROPER, A. STINE, B. VIERRA, AND K. ZHU. 2012. Individual-scale inference to anticipate climate-change vulnerability of biodiversity. Philosophical Trans. Royal Soc. B 367: 236–246.

CLINTON, B. D. AND C. R. BAKER. 1999. Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses. For. Ecol. Manage. 126: 51–60.

CORNELISSEN, J., R. AERTS, B. CERABOLINI, M. WERGER, AND M. VAN DER HEIJDEN. 2001. Carbon cycling traits of plant species are linked with mycorrhizal strategy. Oecologia 129: 611–619.

COYLE, D. R., T. E. NEBEKER, E. R. HART, AND W. J. MATTSON. 2005. Biology and management of insect pests in North American intensively managed hardwood forest systems. Ann. Rev. Entomol. 50: 1–29.

DALE, V. H., M. L. THARP, K. O. LANNOM, AND D. G. HODGES. 2010. Modeling transient response of forests to climate change. Sci. Tot. Environ. 408: 1888–1901.

DE FRENNE, P., A. KOLB, K. VERHEYEN, J. BRUNET, O. CHABRERIE, G. DECOCQ, M. DEIKMANN, O. ERIKSSON, T. HEINKEN, M. HERMY, Ü. JÕGAR, S. STANTON, P. QUATAERT, R. ZINDEL, M. ZOBEL, AND B. J. GRAAE. 2009. Unravelling the effects of temperature, latitude and local environment on the reproduction of forest herbs. Global Ecol. Biogeogr. 18: 641–651.

DUFFEY, D. C. AND A. J. MEIER. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? Conserv. Biol. 6: 196–201.

DYER, J. M. 2010. Land-use legacies in a central Appalachian forest: differential response of trees and herbs to historic agricultural practices. Appl. Veg. Sci. 13: 195–206.

ELLIOTT, K. J., L. R. BORING, W. T. SWANK, AND B. R. HAINES. 1997. Successional changes in diversity and composition in a clearcut watershed in Coweeta Basin, North Carolina. For. Ecol. Manage. 92: 67–85.

ELLIOTT, K. J., L. R. BORING, AND W. T. SWANK. 1998. Changes in vegetation diversity following grass-to-forest succession. Am. Midl. Nat. 140: 219–232.

ELLIOTT, K. J., S. L. HITCHCOCK, AND L. KRUEGER. 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: hurricane opal and salvage logging. J. Torrey Bot. Soc. 129: 48–59.

ELLIOTT, K. J. AND J. D. KNOEPP. 2005. The effects of three regeneration harvest methods on plant diversity and soil characteristics in the southern Appalachians. For. Ecol. Manage. 211: 296–317.

ELLIOTT, K. J., J. M. VOSE, J. D. KNOEPP, D. W. JOHNSON, W. T. SWANK, AND W. JACKSON. 2008. Simulated Effects of Sulfur Deposition on Nutrient Cycling in Class I Wilderness Areas. J. Environ. Qual. 37: 1419–1431.

ELLIOTT, K. J., B. COLLINS, AND C. A. HARPER. 2011. Herbaceous response to type and severity of disturbance, p. 97–110. *In* C. Greenberg, B. Collins, and F. Thompson, III [eds.], Sustaining Young Forest Communities. Springer Series: Managing Forest Ecosystems, Volume 21, Springer, New York, NY.

FEDERER, C. A., J. W. HORNBECK, L. M. TRITTON, C. W. MARTIN, R. S. PIERCE, AND C. T. SMITH. 1989. Long-term depletion of calcium and other nutrients in eastern US forests. Environ. Manage. 13: 593–601.

FLINN, K. M. AND M. VELLEND. 2005. Recovery of forest plant communities in post-agricultural landscapes. Front. Ecol. Environ. 3: 243–250.

FLORY, S. L. AND K. CLAY. 2010. Non-native grass invasion alters native plant composition in experimental communities. Biol. Invasions 12: 1285–1294.

Ford, W. M., R. H. Odom, P. E. Hale, and B. R. Chapman. 2000. Stand-age, stand characteristics, and landform effects on understory herbaceous communities in southern Appalachian cove-hardwoods. Biol. Conserv. 93: 237–246.

Ford, C. R., S. J. Laseter, W. T. Swank, and J. M. Vose. 2011. Can forest management be used to sustain water-based ecosystem services in the face of climate change? Ecol. Appl. 21: 2049–2067.

Ford, C. R., K. J. Elliott, B. D. Clinton, B. D. Kloeppel, and J. M. Vose. 2012. Changes in southern Appalachian riparian forest community structure and composition following eastern hemlock mortality. Oikos 121: 523–536.

Foster, D. R., J. D. Aber, J. M. Melillo, R. D. Bowden, and E. A. Bazzaz. 1997. Forest response to disturbance and anthropogenic stress. BioScience 47: 437–444.

Fraterrigo, J. M., S. M. Pearson, and M. G. Turner. 2009a. Joint effects of habitat configuration and temporal stochasticity on population dynamics. Landscape Ecol. 24: 863–877.

Fraterrigo, J. M., S. M. Pearson, and M. G. Turner. 2009b. The response of understory herbaceous plants to nitrogen fertilization in forests of different land-use history. For. Ecol. Manage. 257: 2182–2188.

Fraterrigo, J. M., M. S. Strickland, A. D. Keiser, and M. A. Bradford. 2011. Nitrogen uptake and preference in a forest understory following invasion by an exotic grass. Oecologia 167: 781–791.

Gaddy, L. L. 1986. Twelve new ant-dispersed species from the southern Appalachians. Bull. Torrey Bot. Club 111: 247–251.

Gibson, D. J., G. Spyreas, and J. Benedict. 2002. Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois. J. Torrey Bot. Soc. 129: 207–219.

Gilliam, F. R. and M. R. Roberts. 2003. The Herbacous Layer in Forests of Eastern North America. Oxford University Press, New York, NY. 464 p.

Gilliam, F. R. 2006. Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. J. Ecol. 94: 1176–1191.

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57: 845–858.

Gilliam, F. S. and D. A. Dick. 2010. Spatial heterogeneity of soil nutrients and plant species in herb-dominated communities of contrasting land use. Plant Ecol. 209: 83–94.

Gilliam, F. S., A. W. Hockenberry, and M. B. Adams. 2006. Effects of atmospheric nitrogen deposition on the herbaceous layer of a central Appalachian hardwood forest. J. Torrey Bot. Soc. 133: 240–254.

Gleason, H. A. and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada, second edition. The New York Botanical Garden, Bronx, NY. 910 p.

Gonzales, E. and J. L. Hamrick. 2005. Distribution of genetic diversity among disjunct populations of the rare forest understory herb, *Trillium reliquum*. Heredity 95: 306–314.

Grace, J. B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. Perspect. Plant Ecol. Evol. Syst. 2: 1–28.

Greenberg, C. H., D. E. McLeod, and D. L. Loftis. 1997. An old growth definition for western and mixed mesophytic forests. General Technical Report SRS-16, Southern Research Station, USDA Forest Service, Asheville, NC. 14 p.

Greenlee, K. W. 1974. A vegetative analysis of a pristine and a selectively cut cove forest of the Unicoi mountains, western North Carolina. M.S. thesis, Western Carolina University, Cullowhee, NC.

Griggs, J. A., J. H. Rock, C. R. Webster, and M. A. Jenkins. 2006. Vegetative legacy of a protected deer herd in Cades Cove, Great Smoky Mountains National Park. Nat. Areas J. 26: 126–136.

Hall, S. L., C. D. Barton, and C. C. Baskin. 2010. Topsoil seed bank of an oak-hickory forest in eastern Kentucky as a restoration tool on surface mines. Restor. Ecol. 18: 834–842.

Hanu, Y. A. K. and D. J. Gibson. 2008. Patterns of invasion: Trends in abundance of understory vegetation, seed rain, and seed bank from forest edge to interior. Nat. Areas J. 28: 228–239.

Hardt, R. A. and W. T. Swank. 1997. A comparison of structural and compositional characteristics of southern Appalachian young second growth, maturing second growth, and old growth stands. Nat. Areas J. 17: 42–52.

Harrison, S., E. I. Damschen, and J. B. Grace. 2010. Ecological contingency in the effects of climatic warming on forest herb communities. Proc. Nat. Acad. Sci. 107: 19362–19367.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, New York, NY. 892 p.

Harrelson, S. M. and G. R. Matlack. 2006. Influence of stand age and physical environment on the herb composition of second-growth forest, Strouds Run, Ohio, USA. J. Biogeogr. 33: 1139–1149.

Hartman, K. M. and B. C. McCarthy. 2008. Changes in forest structure and species composition following invasion by a non-indigenous shrub, Amur honeysuckle (*Lonicera maackii*). J. Torrey Bot. Soc. 135: 245–259.

Hawkins, T. S., J. M. Baskin, and C. C. Baskin. 2007. Seed morphology, germination phenology, and capacity to form a seed bank in six herbaceous layer Apiaceae species of the Eastern Deciduous Forest. Castanea 72: 8–14.

Holzmueller, E. J., S. Jose, and M. A. Jenkins. 2009. The response of understory species composition, diversity, and seedling regeneration to repeated burning in Southern Appalachian oak-hickory forests. Nat. Areas J. 29: 255–262.

Houle, G. 1994. Spatiotemporal patterns in the components of regeneration of four sympatric tree species – *Acer rubrum*, *A. saccharum*, *Betula alleghaniensis and Fagus grandifolia*. J. Ecol. 82: 39–53.

HOULE, G. 2007. Determinants of fine-scale plant species richness in a deciduous forest of northeastern North America. J. Veg. Sci. 18: 345–354.

HUEBNER, C. D. 2011. Seed mass, viability, and germination of Japanese Stiltgrass (*Microstegium vimineum*) under variable light and moisture conditions. Invasive Plant Sci. Manage. 4: 274–283.

HUSTON, M. A. 1994. Biological Diversity: The coexistence of species on changing landscapes. Cambridge University Press, Cambridge, UK. 681 p.

HUTCHINSON, T. F., R. E. J. BOERNER, L. R. IVERSON, S. SUTHERLAND, AND E. K. SUTHERLAND. 1999. Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (U.S.A.) *Quercus* forests. Plant Ecol. 144: 179–189.

HUTCHINSON, T. F., R. E. J. BOERNER, S. SUTHERLAND, E. K. SUTHERLAND, M. ORTT, AND L. R. IVERSON. 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. Can. J. For. Res. 35: 877–890.

IPCC. 2007. Climate change 2007: the physical science basis. *In* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L Miller [eds.], Contribution of Working Group I to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

JACKSON, B. C., J. D. PITTILLO, H. L. ALLEN, T. R. WENTWORTH, B. P. BULLOCK, AND D. L. LOFTIS. 2009. Species diversity and composition in old growth and second growth rich coves of the Southern Appalachian Mountains. Castanea 74: 27–38.

JENKINS, M. A. AND G. R. PARKER. 2000. The response of herbaceous-layer vegetation to anthropogenic disturbance in intermittent stream bottomland forests of southern Indiana, USA. Plant Ecol. 151: 223–237.

JULES, E. S. 1998. Habitat fragmentation and demographic change for a common plant: *Trillium* in old-growth forest. Ecology 79: 1645–1656.

KIMMINS, J. P. 1997. Forest Ecology: a foundation for sustainable management. Prentiss-Hall, Inc., Upper Saddle River, NJ. 596 p.

KRAPFL, K. J., E. J. HOLZMUELLER, AND M. A. JENKINS. 2012. Understory composition of five Tsuga canadensis associated communities in Great Smoky Mountains National Park. Nat. Areas J. 32: 260–269.

KRUEGER, L. M. AND C. J. PETERSON. 2009. Effects of woody debris and ferns on herb-layer vegetation and deer herbivory in a Pennsylvania forest blowdown. EcoScience 16: 461–469.

KUDOH, H., H. SHIBAIKE, H. TAKASU, D. F. WHIGHAM, AND S. KAWANO. 1999. Genet structure and determinants of clonal structure in a temperate deciduous woodland herb, *Uvularia perfoliata*. J. Ecol. 87: 244–257.

LASETER, S. H., C. R. FORD, J. M. VOSE, AND L. W. SWIFT JR. 2012. Long-term temperature and precipitation trends at the Coweeta Hydrologic Laboratory, Otto, North Carolina, USA. Hydrology Res. 43: 890–901.

LATA, H., R. M. MORAES, A. DOUGLAS, AND B. E. SCHEFFLER. 2002. Assessment of genetic diversity in *Podophyllum peltatum* by molecular markers, p. 537–544. *In* J. Janick and A. Whipkey [eds.], Trends in New Crops and New Uses. ASHA Press, Alexandria, VA.

LAWRENCE, G. B., W. C. SHORTLE, M. B. DAVID, K. T. SMITH, R. A. F. WARBY, AND A. G. LAPENSIS. 2012. Early indications of soil recovery from acidic deposition in U.S. red spruce forests. Soil Sci. Soc. Am. J. 76: 1407–1417.

LEEGE, L. M., J. S. THOMPSON, AND D. J. PARRIS. 2010. The responses of rare and common Trilliums (*Trillium reliqium*, *T. cuneatum*, and *T. maculatum*) to deer herbivory and invasive honeysuckle removal. Castanea 75: 433–443.

LEVINE, M. T. AND I. C. FELLER. 2004. Effects of forest age and disturbance on population persistence in the understory herb, *Arisaema triphyllum* (Araceae). Plant Ecol. 72: 73–82.

LOVETT, G. M., C. D. CANHAM, M. A. ARTHUR, K. C. WEATHERS, AND R. D. FITZHUGH. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 56: 395–405.

MARTIN, K. L. AND P. C. GOEBEL. 2013. The foundation species influence of eastern hemlock (Tsuga canadensis) on biodiversity and ecosystem function on the Unglaciated Allegheny Plateau. For. Ecol. Manage. 289: 143–152.

MARTIN, P. H., C. D. CANHAM, AND P. L. MARKS. 2009. Why forests appear resistant to exotic plant invasions: intentional introductions stand dynamics, and the role of shade tolerance. Front. Ecol. Environ. 7: 142–149.

MATYSSEK, R., G. WIESER, C. CALFAPIETRA, W. DE VRIES, P. DIZENGREMEL, D. ERNST, Y. JOLIVET, T. N. MIKKELSEN, G. M. J. MOHREN, D. LE THIEC, J.-P. TUOVINEN, A. WEATHERALL, AND E. PAOLETTI. 2012. Forests under climate change and air pollution: Gaps in understanding and future directions for research. Environ. Poll. 160: 57–65.

MCCARTHY, B. C. 2003. The herbaceous layer of eastern old-growth deciduous forests, p. 163–176. *In* F. R. Gilliam and M. R. Roberts [eds.], The Herbacous Layer in Forests of Eastern North America. Oxford University Press, New York, NY.

MCEWAN, R. W. AND R. N. MULLER. 2011. Dynamics, diversity, and resource gradient relationships in the herbaceous layer of an old-growth Appalachian forest. Plant Ecol. 212: 1179–1191.

MCLACHLAN, S. M. AND D. H. BAZELY. 2001. Recovery patterns of understory herbs and their use as indicators of deciduous forest regeneration. Conserv. Biol. 15: 98–110.

MCNAB, W. H. AND D. L. LOFTIS. 2002. Probability of occurrence and habitat features for oriental bittersweet in an oak forest in the southern Appalachian Mountains, USA. For. Ecol. Manage. 155: 45–54.

MEIER, A. J., S. P. BRATTON, AND D. C. DUFFEY. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. Ecol. Appl. 5: 935–946.

Miller, K. E. and D. L. Gorchov. 2004. The invasive shrub, *Lonicera maackii*, reduces growth and fecundity of perennial forest herbs. Oecologia 139: 359–375.

Mitchell, C. E., M. G. Turner, and S. M. Pearson. 2002. Effects of historical land use and forest patch size on myrmecochores and ant communities. Ecol. Appl. 12: 1364–1377.

Moore, J. E., S. B. Franklin, G. Wein, and B. S. Collins. 2012. Long-term population demography of *Trillium recurvatum* on loess bluffs in western Tennessee, USA. AoB Plants. doi:10.1093/aobpla/pls0.15.

Monk, C. D., D. T. McGinty, and F. P. Day Jr. 1985. The ecological importance of *Kalmia latifolia* and *Rhododendron maximum* in the deciduous forests of the southern Appalachians. Bull. Torrey Bot. Club 112: 187–193.

Nelson, C. R., C. Halpern, and J. A. Antos. 2007. Variation in responses of late-seral herbs to disturbance and environmental stress. Ecology 88: 2880–2890.

Newell, C. L., R. K. Peet, and J. C. Harrod. 1997. Vegetation of Joyce Kilmer-Slickrock Wilderness, North Carolina. Curriculum in Ecology & Department of Biology, University of North Carolina, Chapel Hill, NC.

Paillet, Y., L. Bergès, J. Hjältén, P. Ódor, C. Avon, M. Bernahardt-Römermann, R.-J. Bijlsma, L. Bruyn, M. Fuhr, U. Grandin, R. Kanka, L. Lundin, S. Luque, T. Magural, S. Matesanz, I. Mészáros, M.-T. Sebastià, W. Schmidt, T. Standovár, T. Tothmérész, A. Uotila, R. Valladares, K. Vellak, and R. Virtanen. 2010. Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. Conserv. Biol. 24: 101–112.

Parr, M. W. 1992. Long-term vegetation response to thinning in a southern Appalachian cove. M.S. thesis, University of Georgia, Athens, GA.

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.

Pedlar, J. H., D. W. McKenney, I. Aubin, T. Beardmore, J. Beaulieu, L. Iverson, G. A. O'Neill, R. S. Winder, and C. Ste-Marie. 2012. Placing forestry in the assisted migration debate. BioScience 62: 835–842.

Peterson, C. J. and J. E. Campbell. 1993. Microsite differences and temporal change in plant communities of treefall pits and mound in an old-growth forest. Bull. Torrey Bot. Club 120: 451–460.

Pittillo, J. D. and M. Lee. 1984. Reference plant collection of the Coweeta Hydrologic Laboratory. General Technical Report SE-29, USDA Forest Service, Southeastern Forest Experiment Station, Asheville, NC. 34 p.

Ristau, T. E., S. H. Stoleson, S. B. Horsley, and D. S. deCalesta. 2011. Ten-year response of the herbaceous layer to an operational herbicide-shelterwood treatment in a northern hardwood forest. For. Ecol. Manage. 262: 970–979.

Rock, J. H., B. Beckage, and L. J. Gross. 2004. Population recovery following differential harvesting of *Allium tricoccum* Ait. in the southern Appalachians. Biol. Conserv. 116: 227–234.

Rodgers, V. L., K. A. Stinson, and A. C. Finzi. 2008. Ready or not, garlic mustard is moving in: *Alliaria petiolata* as a member of eastern North American forests. BioScience 58: 426–436.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2000. MetaWin. Statistical Software for Meta-Analysis. 2.0 ed. Sinauer Associates, Sunderland, MA.

Royo, A. A., S. L. Stout, D. S. deCalesta, and T. G. Pierson. 2010. Restoring forest herb communities through landscape-level deer herd reductions: Is recovery limited by legacy effects? Biol. Conserv. 143: 2425–2434.

Sanders, S. and J. B. McGraw. 2005. Harvest recovery of goldenseal, *Hydrastis canadensis* L. Am. Midl. Nat.153 87–94.

Sawyer, N. W. 2010. Reproductive ecology of *Trillium recurvatum* (Trilliaceae) in Wisconsin. Am. Midl. Nat. 163: 146–160.

Schafale, M. P. and A. S. Weakley. 1990. Classification of the natural communities of North Carolina, 3rd approximation. North Carolina Heritage Program, Raleigh, NC. 321 p.

Schramm, J. W. and J. G. Ehrenfeld. 2010. Leaf litter and understory canopy shade limit the establishment, growth and reproduction of *Microstegium vimineum*. Biol. Invasions 12: 3195–3204.

Scott, A. J. and J. W. Morgan. 2012. Early life history stages drive community reassembly in Australian old-fields. J. Veg. Sci. 23: 721–731.

Shields, J. M. and C. R. Webster. 2007. Ground-layer response to group selection with legacy-tree retention in a managed northern hardwood forest. Can. J. For. Res. 37: 1797–1807.

Simon, S. A., T. K. Collins, G. L. Kauffmann, W. H. McNab, and C. J. Ulrey. 2005. Ecological zones in the southern Appalachians: First approximation. Research Paper SRS-41, USDA Forest Service, Southern Research Station, Asheville, NC. 41 p.

Singleton, R., S. Gardescu, S. L. Marks, and M. A. Geber. 2001. Forest herb colonization of post-agricultural forests in central New York State, USA. J. Ecol. 89: 325–338.

Small, C. J. and B. C. McCarthy. 2002. Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest. Plant Ecol. 164: 37–48.

Small, C. J. and B. C. McCarthy. 2005. Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. For. Ecol. Manage. 217: 222–243.

Small, C. J. and B. C. McCarthy. 2010. Seed bank variation under contrasting site quality conditions in mixed oak forests of southeastern Ohio, USA. Internatl. J. For. Res.: doi:10.1155/2010/419482.

Small, C. J., J. L. Chamberlain, and D. S. Mathews. 2011. Recovery of black cohosh (*Actaea racemosa* L.) following experimental harvests. Am. Midl. Nat. 166: 339–348.

SORRELLS, J. AND R. J. WARREN II. 2011. Ant-dispersed herb colonization lags behind forest re-establishment. J. Torrey Bot. Soc. 138: 77–84.

THOMAS, D. J. 1996. Soil Survey of Macon County, North Carolina. USDA Nat. Res. Conserv. Serv., U.S. Government Printing Office, Washington, DC. 322 p.

THIEMANN, J. A., C. R. WEBSTER, M. A. JENKINS, P. M. HURLEY, J. H. ROCK, AND P. S. WHITE. 2009. Herbaceous-layer impoverishment in a post-agricultural southern Appalachian landscape. Am. Midl. Nat. 162: 148–168.

ULREY, C. J. 2002. The relationship between soil fertility and the forests of the Southern Appalachian Region. Ph.D. Dissertation, North Carolina State University, Raleigh, NC.

VAN DER VOORT, M., B. BAILEY, D. E. SAMUEL, AND J. B. MCGRAW. 2003. Recovery of populations of goldenseal (*Hydrastis canadensis* L.) and American ginseng (*Panax quinquefolius* L.) following harvest. Am. Midl. Nat. 149: 282–292.

VELLEND, M., K. VERHEYEN, K. M. FLINN, H. JACQUEMYN, A. KOLB, H. VAN CALSTER, G. PETERKEN, B. J. GRAAE, J. BELLEMARE, O. HONNAY, J. BRUNET, M. WULF, F. GERHARDT, AND M. HERMY. 2007. Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use. J. Ecol. 95: 565–573.

VITT, P., K. HAVENS, AND O. HOEGH-GULDBERG. 2009. Assisted migration: part of an integrated conservation strategy. Trends Ecol. Evol. 24: 473–474.

WARREN, R. J., V. BAHN, AND M. A. BRADFORD. 2011. Temperature cues phenological synchrony in ant-mediated seed dispersal. Global Change Biol. 17: 2444–2454.

WEBSTER, C. R. AND M. A. JENKINS. 2008. Age structure and spatial patterning of *Trillium* populations in old-growth forests. Plant Ecol. 199: 43–54.

WELCH, N. T., J. M. BELMONT, AND J. C. RANDOLPH. 2007. Summer ground layer biomass and nutrient contribution to above-ground litter in an Indiana temperate deciduous forest. Am. Midl. Nat. 157: 11–26.

WHIGHAM, D. F. 2004. Ecology of woodland herbs in temperate deciduous forests. Ann. Rev. Ecol. Evol. Syst. 35: 583–621.

WHIGHAM, D. F., J. P. O'NEILL, H. N. RASMUSSEN, B. A. CALDWELL, AND M. K. MCCORMICK. 2006. Seed longevity in terrestrial orchids – Potential for persistent in situ seed banks. Biol. Conserv. 129: 24–30.

WHITTAKER, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26: 1–69.

WHITTAKER, R. J. 2010. Meta-analyses and mega-mistakes: calling time on meta-analysis of the species richness–productivity relationship. Ecology 91: 2522–2533.

WHITTAKER, R. H. AND S. A. LEVIN. 1977. The role of mosaic phenomena in natural communities. Theor. Pop. Biol. 12: 117–139.

WILLSON, M. 1993. Dispersal mode, seed shadows and colonization patterns. Vegetatio 107/108: 261–280.

WURZBURGER, N. AND R. L. HENDRICK. 2007. Rhododendron thickets alter N cycling and soil extracellular enzyme activity in southern Appalachian hardwood forests. Pedobiologia 50: 563–576.

WYATT, J. L. AND M. R. SILMAN. 2010. Centuries-old logging legacy on spatial and temporal patterns in understory herb communities. For. Ecol. Manage. 260: 116–124.

ZELIKOVA, T. J., R. R. DUNN, AND N. J. SANDERS. 2008. Variation in seed dispersal along an elevational gradient in Great Smoky Mountains National Park. Acta Oecologia 34: 155–162.

ZENNER, E. K., M. A. MARTIN, B. J. PALIK, J. E. PECK, AND C. R. BLINN. 2012. Response of herbaceous plant community diversity and composition to overstorey harvest within riparian management zones in Northern Hardwoods. Forestry doi: 10.1093/forestry/cps060.

Appendix A. Herbaceous-layer species in mesic forests of six watersheds in the Coweeta Basin. Herbaceous species and woody species are presented separately for cover, biomass, and number of species. All herbaceous species with ≥ 0.9% relative cover (cover of the *i*th species ÷ total cover) are listed by rank abundance. Standard errors are in parentheses.

WS28 (sample year 1991) 16 plots, quadrat size = 4*(1.0 m^2)

Herbaceous species	Cover %	Relative Cover %
Thelypteris noveboracensis	7.98 (1.85)	22.07
Laportea canadensis	4.37 (1.64)	12.07
Viola spp.	2.83 (0.91)	7.82
Thalictrum calavatum	2.21 (0.56)	6.11
Aster divaricatus [syn. *Eurybia divaricata* (L.) Nesom]	2.20 (0.38)	6.07
Tiarella cordifolia	2.08 (0.58)	5.75
Solidago curtisii	1.93 (0.34)	5.34
Polystichum acrostichoides	1.44 (0.56)	3.97
Thelypteris hexagonoptera	1.20 (0.35)	3.33
Viola rotundifolia	1.10 (0.50)	3.04
Galium spp.	1.08 (0.28)	2.99
Anthrocarpa bracteata	0.79 (0.47)	2.18
Dioscorea villosa	0.70 (0.15)	1.92
Arisaema triphyllum	0.67 (0.16)	1.86
Uvularia perfoliata	0.63 (0.38)	1.75
Eupatorium rugosum	0.59 (0.31)	1.62
Desmodium nudiflorum	0.49 (0.26)	1.4
Monarda clinopoda	0.48 (0.24)	1.3
Orchis spectabilis	0.44 (0.16)	1.2
Actaea pachypoda	0.44 (0.21)	1.2
Botrychium virginianum	0.39 (0.14)	1.1
Caulophyllum thalictroides	0.34 (0.21)	0.9
Total cover %	36.18 (4.32)	
Number of herb species =	41	

Woody species	Relative basal area (%)
Acer rubrum	18
Tilia heterophylla	17
Betula lenta	13
Betula alleghaniensis	11
Liriodendron tulipifera	9
Acer saccharum	7
Tsuga canadensis	7
Number of woody species =	20
Total number of species =	61

WS34 (sample year 1999) 12 plots, quadrat size = 4*(1.0 m^2)

	Hurricane + salvage		Reference	
Herbaceous species	Percent cover (SE)	Relative Cover %	Percent cover (SE)	Relative Cover %
Smilacina racemosa	6.50 (3.55)	11.1	1.92 (0.92)	15.3
Impatiens capensis	5.73 (2.65)	9.8	–	–
Cimicifuga racemosa	4.22 (1.18)	7.2	0.08 (0.08)	0.6
Galium lanceolatum	3.27 (0.97)	5.6	0.04 (0.04)	0.3
Viola spp.	3.19 (1.53)	5.4	0.001 (0.001)	0.01
Sanguinaria canadensis	2.15 (0.73)	3.7	–	–
Arisaema triphyllum	2.06 (0.50)	3.5	0.38 (0.29)	3.0
Eupatorium rugosum	2.04 (0.42)	3.5	0.29 (0.20)	2.3
Pycnanthemum incanum	1.97 (0.89)	3.4	–	–
Desmodium nudiflorum	1.96 (0.72)	3.4	1.21 (0.67)	9.6
Solidago curtisii	1.90 (0.64)	3.2	0.83 (0.40)	6.6
Dichanthelium sp.	1.69 (0.77)	2.9	1.21 (0.60)	9.6
Oxalis stricta	1.60 (1.05)	2.7	0.12 (0.12)	1.0
Botrychium virginianum	1.27 (1.03)	2.2	–	–
Aster divaricatus	1.21 (0.53)	2.1	0.12 (0.12)	1.0
Disporum lanuginosum	1.05 (0.23)	1.8	–	–
Lysimachia quadrifolia	0.96 (0.31)	1.6	0.58 (0.30)	4.6
Polygonatum biflorum	0.94 (0.37)	1.6	0.04 (0.04)	0.3
Dioscorea villosa	0.87 (0.33)	1.5	0.04 (0.04)	0.3
Monarda clinopodia	0.83 (0.27)	1.4	–	–
Trillium sp.	0.80 (0.21)	1.4	0.08 (0.08)	0.6
Polystichum acrostichoides	0.62 (0.52)	1.1	0.50 (0.30)	4.0
Viola rotundifolia	0.58 (0.25)	1.0	0.96 (0.62)	7.6
Total cover (%)	58.57 (6.87)		12.56 (4.27)	
Number of herb species =	66		42	

Woody species	Percent cover (SE)	Relative Cover %	Percent cover (SE)	Relative Cover %
Parthenocissus quinquefolia	15.79 (3.94)	35.1	3.00 (1.94)	26.4
Smilax rotundifolia	5.81 (2.44)	12.9	0.002 (0.002)	0.02
Clematis virginiana	4.62 (2.00)	10.3	–	–
Quercus rubra	4.21 (1.78)	9.4	1.29 (0.63)	11.3
Vitis sp.	3.42 (1.51)	7.6	–	–
Rubus alleghanensis	3.27 (1.74)	7.3	0.04 (0.04)	0.4
Carya sp.	3.02 (1.76)	6.7	0.12 (0.12)	1.0
Aristolochia macrophylla	2.54 (1.37)	5.6	1.12 (0.37)	1.0
Prunus serotina	1.44 (0.41)	3.2	0.29 (0.19)	2.5
Acer rubrum	1.27 (0.66)	2.8	0.46 (0.32)	4.0
Fraxinus americana	1.00 (0.55)	2.2	$<$0.001	$<$0.01
Total cover (%)	44.98 (4.83)		11.38 (3.12)	
Number of woody species =	26		19	
Total number of species =	92		61	

WS7 (sample year 2008) 14 plots, quadrat size = 2*(1.0 m^2)

Herbaceous species	Cover % (SE)	Relative cover (%)	Mass g/m^2 (SE)	Relative Mass (%)
Polystichum acrostichoides	2.18 (0.85)	22.4	3.48 (1.69)	36.8
Solidago curtisii	1.93 (1.78)	19.8	3.24 (3.19)	34.2
Carex sp.	0.75 (0.53)	7.7	0.57 (0.49)	6.0
Thelypteris noveboracensis	0.71 (0.71)	7.3	0.33 (0.33)	3.5
Viola spp.	0.72 (0.23)	7.4	0.23 (0.08)	2.4
Polygonatum biflorum	0.61 (0.53)	6.2	0.62 (0.61)	6.6
Arisaema triphyllum	0.50 (0.20)	5.1	0.15 (0.05)	1.6
Smilax glauca	0.31 (0.14)	3.2	0.13 (0.05)	1.4
Aster divaricatus	0.14 (0.11)	1.4	0.04 (0.04)	0.4
Galium latifolium	0.14 (0.11)	1.4	0.03 (0.02)	0.3
Total cover (%) or mass (g/m^2)	9.73 (3.12)		9.46 (4.93)	
Number of herb species =	37			

Woody species	Cover % (SE)	Relative cover (%)	Mass g/m^2 (SE)	Relative Mass (%)
Smilax rotundifolia	0.82 (0.29)	25.0	0.74 (0.32)	24.3
Parthenocissus quinquefolia	1.00 (0.44)	21.4	0.66 (0.52)	21.6
Quercus montana	0.92 (0.52)	19.6	0.62 (0.37)	20.3
Rubus sp.	0.68 (0.38)	14.5	0.21 (0.12)	6.9
Rhododendron maximum	0.18 (0.18)	3.8	0.38 (0.38)	12.4
Symplocos tinctoria	0.18 (0.18)	3.8	0.09 (0.09)	2.9
Quercus coccinea	0.14 (0.14)	3.0	0.08 (0.08)	2.6
Total cover (%) or mass (g/m^2)	4.68 (0.87)		3.05 (0.65)	
Number of woody species =	19			
Total number of species =	56			

WS6 (sample year 1995) 20 plots, quadrat size = 2*(1.0 m^2)

Herbaceous species	Cover % (SE)	Relative cover (%)	Mass g/m^2 (SE)	Relative Mass (%)
Eupatorium rugosum	33.55 (4.33)	56.7	20.93 (3.36)	57.8
Polystichum acrostichoides	5.18 (1.66)	8.7	6.76 (2.89)	18.7
Dennstaedtia punctilobula	3.72 (1.86)	6.3	1.57 (0.72)	4.3
Adiantum pedatum	3.42 (2.07)	5.8	1.35 (0.75)	3.7
Dichanthelium sp.	2.38 (0.63)	4.0	0.99 (0.36)	2.7
Desmodium nudiflorum	1.40 (0.60)	2.4	0.33 (0.18)	0.9
Ranunculus hispidus	1.18 (0.82)	2.0	0.63 (0.54)	1.7
Porteranthus trifoliatus	1.04 (0.31)	1.8	0.41 (0.19)	1.1
Poa spp.	0.98 (0.55)	1.6	0.63 (0.42)	1.7
Tiarella cordifolia	0.63 (0.22)	1.1	0.08 (0.03)	0.2
Total cover (%) or mass (g/m^2)	59.21 (4.13)		36.21 (4.37)	
Number of herb species =	38			

Woody species	Cover % (SE)	Relative cover (%)	Mass g/m^2 (SE)	Relative Mass (%)
Rubus sp.	8.25 (2.37)	55.9	6.22 (1.99)	42.4
Smilax rotundifolia	4.18 (1.88)	28.3	7.33 (2.95)	50.0
Lonicera japonica	1.08 (0.63)	7.3	0.38 (0.21)	2.6
Parthenocissus quinquefolia	0.34 (0.17)	2.3	0.06 (0.05)	0.4
Acer rubrum	0.14 (0.07)	0.9	0.05 (0.03)	0.3
Liriodendron tulipifera	0.10 (0.08)	0.7	0.04 (0.03)	0.3
Total cover (%) or mass (g/m^2)	14.76 (2.72)		14.65 (3.58)	
Number of woody species =	18			
Total number of species =	56			

WS13 (sample year 1992) 15 plots, quadrat size = 4*(1.0 m^2)

Herbaceous species	Cover % (SE)	Relative cover (%)
Polystichum acrostichoides	2.47 (1.09)	18.3
Viola rotundifolia	1.70 (0.86)	12.6
Athyrium felix-femina	1.23 (0.77)	9.1
Arisaema triphyllum	1.20 (0.63)	8.9
Smilax glauca	1.07 (0.22)	7.9
Galium latifolium	0.95 (0.91)	7.0
Thelypteris noveboracensis	0.92 (0.65)	6.8
Adiantum pedatum	0.55 (0.42)	4.1
Medeola virginiana	0.33 (0.32)	2.4
Viola spp.	0.22 (0.17)	1.6
Osmunda cinnamomea	0.17 (0.12)	1.2
Total cover (%)	13.50 (4.20)	
Number of herb species =	40	

Woody species	Cover % (SE)	Relative cover (%)
Smilax rotundifolia	0.60 (0.18)	17.5
Acer rubrum	0.55 (0.23)	16.0
Parthenocissus quinquefolia	0.26 (0.14)	7.6
Liriodendron tulipifera	0.25 (0.08)	7.3
Pyrularia pubera	0.23 (0.18)	6.7
Amelanchier arborea	0.13 (0.07)	3.8
Total cover (%)	3.43 (0.46)	
Number of woody species =	24	
Total number of species =	64	

Reynolds reference (sample year 1998) 40 transects, 20 m length each

Herbaceous species	Cover % (SE)	Relative cover (%)
Thelypteris noveboracensis	15.42 (2.01)	46.1
Tiarella cordifolia	2.64 (0.37)	7.9
Viola spp. (*blanda, cucullata,hastata*)	2.45 (0.33)	7.3
Thelypteris hexagonoptera	1.72 (0.28)	5.1
Thalictrum dioicum	1.01 (0.22)	3.0
Solidago curtisii	0.91 (0.15)	2.7
Desmodium nudiflorum	0.80 (0.17)	2.4
Osmunda spp. (*cinnamomea, claytonia*)	0.72 (0.47)	2.2
Medeola virginiana	0.71 (0.16)	2.1
Eupatorium rugosum	0.70 (0.20)	2.1
Polystichum acrostichoides	0.65 (0.18)	2.0
Disporum lanuginosum	0.65 (0.13)	2.0
Aster divaricatus	0.57 (0.10)	1.7
Prenanthes trifoliolata	0.41 (0.08)	1.2
Arisaema triphyllum	0.35 (0.10)	1.0
Dioscorea villosa	0.34 (0.09)	1.0
Veratrum parviflorum	0.34 (0.08)	1.0
Actaea pachypoda	0.30 (0.10)	0.9
Total cover (%)	33.44 (2.54)	
Number of herb species =	61	

Woody species	Cover % (SE)	Relative cover (%)
Viburnum acerifolium	1.00 (0.31)	14.0
Rhododendron maximum	0.83 (0.33)	11.6
Parthenocissus quinquefolia	0.76 (0.22)	10.6
Acer rubrum	0.71 (0.15)	9.9
Fraxinus americana	0.58 (0.18)	8.1
Acer pensylvanicum	0.58 (0.09)	8.1
Smilax rotundifolia	0.51 (0.12)	7.1
Carya spp.	0.35 (0.10)	4.9
Rubus sp.	0.15 (0.10)	2.1
Quercus rubra	0.12 (0.05)	1.6
Total cover (%)	7.14 (0.84)	
Number of woody species =	28	
Total number of species =	89	