Composition and Structure of Two Old-growth Forest Ecosystem Types of Southeastern Ohio[1]

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Abstract. Less than 1% of the pre-European settlement forest in Ohio currently remains, mostly as small and scattered woodlots. Consequently, few studies have been undertaken to quantify the composition and structure of Ohio's old-growth forests using a landscape ecosystem perspective. We used an existing multifactor ecosystem classification system developed for the Wayne National Forest in southeastern Ohio to compare the composition and structure of two old-growth forest ecosystem types, located on contrasting north-facing and south-facing middle slopes. No differences in physiography were observed among the stands other than aspect; however, the north-facing old-growth ecosystem type had a greater A horizon thickness and a higher pH than the south-facing old-growth ecosystem type. Mixed-oaks dominate the south-facing ecosystem type, while sugar maple, American beech and northern red oak dominate the north-facing ecosystem type. No differences were detected in stand structural components. Similar trends were observed for the ground-flora layer; specifically, we observed differences in ground-flora composition between the two ecosystem types but no differences in total percent cover or species richness. Finally, the composition and structure of coarse woody debris differed between the contrasting ecosystem types. Maple and oak snags and fallen logs dominate the north-facing ecosystem while oak standing snags and fallen stems are typically observed in the south-facing ecosystem. Few differences between the two ecosystem types were detected in coarse woody debris structure, except that snag density tends to be higher in the south-facing old-growth ecosystem and log density and volume tends to be higher in the north-facing ecosystem (*P* <0.10). Through the use of this ecosystem approach, we can begin to quantify the ecological factors regulating the composition and structure of old-growth communities, improving our ability to effectively manage and restore these rare ecosystems.

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INTRODUCTION

Although humans and forest ecosystems often interact in complex and synergistic ways, individual old-growth stands or forests typically represent an undisturbed condition where the influence of geomorphology, soils, and natural disturbances, in conjunction with plant reproductive processes and animals, constrain the development of plant communities (Rowe and Sheard 1981; Pregitzer and others 2001). Old-growth forests are generally considered to represent the final, stable phase of stand development and typically are recognized by the unique structural characteristics they share. For example, eastern old-growth forests are usually described as multi-aged stands with multiple structural layers, large amounts of coarse woody debris (both dead snags and fallen logs), undisturbed soils, and a diverse array of both plants and animals (Parker 1989; Leverett 1996). Ecosystem processes, including nutrient cycling, stability, and biodiversity, are also believed to remain undisturbed in old-growth forests (Leverett 1996; Meier and others 1996).

In Ohio, as well as across the Central Hardwoods Region, the remaining isolated old-growth tracts have been the focus of old-growth preservation and recovery programs (Trombulak 1996). These remnant and isolated woodlots may be seen as analogous to museum archives, revealing little about the overall landscape or interactions among forest ecosystems at the time of European settlement. Additionally, many of these remnant old-growth stands are in transition. Land-use practices in the surrounding landscape, such as fire suppression, are resulting in compositional and structural changes in these old-growth forests (Goebel and Hix 1996, 1997). Because the composition and structure of individual old-growth stands is influenced strongly by the dispersal patterns of individual species, site history, and environmental factors, the focus of old-growth preservation must occur at the ecosystem level and focus on preserving the 'natural' processes of old-growth forests (Barnes 1989; Pickett and Parker 1994; Trombulak 1996).

Ecosystem classification is a useful tool that facilitates the understanding of interrelationships among plant communities and the environment and how these factors influence ecosystem restoration decisions (Palik and others 2000). Ecosystem classifications define ecosystems hierarchically, as volumes of earth, air, and water with specific developmental histories in which plants and animals live and interact (Rowe and Barnes 1994; Barnes and others 1998). In Ohio, there has been some research published concerning the composition and structure of particular old-growth tracts (for example, McCarthy and others 1987; Cho and Boerner 1991; McCarthy and others 2001). However, very little is known about the compositional and structural variation among Ohio's old-growth forest ecosystems in relation to the hierarchical

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factors regulating their composition and structure, especially physiography and soils. By applying the ecosystem classifications developed for the Wayne National Forest (Hix and Pearcy 1997; Hix and others 1997), old-growth conditions of individual forest ecosystems of southeastern Ohio can be described and compared, ultimately leading to improved programs to manage and restore these threatened ecosystems.

Using the ecosystem classification developed for the Athens Unit of the Wayne National Forest as a framework, in this paper we: 1) examine the physiographic and edaphic factors that regulate overstory and ground-flora vegetation of two old-growth forest ecosystems in southeastern Ohio; and 2) examine the physiographic constraints on coarse woody debris (CWD) composition and structure between the two old-growth forest ecosystems.

MATERIALS AND METHODS

Study Area

The study area is located in the Western Hocking Plateau Subsection (221Ef) of the Southern Unglaciated Allegheny Plateau Section (221E) in the Eastern Broadleaf Forest Province (Keys and others 1995). The Subsection is described as a maturely dissected plateau with moderate to steep slopes, narrow ridgetops, rock outcrops, and narrow stream valleys with elevations ranging from 195 to 322 m above sea level. Geology of the study area consists of inter-bedded sedimentary bedrock of shale, siltstone, limestone, and coal that was laid down in the shallow seas of the Mississippian, Pennsylvanian, or Permian periods in an anticline that dips eastward to the Appalachian Geosyncline (Rypma 1961; Keys and others 1995). In general, the soils are moderately acidic with surface layers that are moderately drained to well-drained loams or silt loams, and with subsoils comprised of silty clays, loamy clays, or clays.

The climate of the area is humid continental with a mean annual temperature of 9° C (Lucht and others 1985). Winters are relatively cold, while summers are generally warm with a mean July maximum temperature of 32.2° C and a mean January minimum temperature of 6.9° C (Athens weather station; Lucht and others 1985). Average annual precipitation is 98 cm, half of which falls from May to October (Lucht and others 1985). The topographic variability associated with the study area is responsible for significant differences in microclimate, which are common. A ridge system oriented from northwest to southeast occurs over most of the study area. This results in southerly-facing slopes that receive higher levels of solar radiation and, consequently, have higher air and soil temperatures, lower relative humidity, and lower soil moisture than their northerly-facing counterparts.

Field Methods

Eight old-growth stands (defined as stands >150 year old; see Goebel and Hix 1996; Olivero and Hix 1998 for information on how these stands were identified) were selected within two contrasting ecosystems using a multifactor ecological classification system (ECS) based on climate, physiography, soils, and vegetation developed recently for the Athens Unit of the Wayne National Forest in southeastern Ohio (Table 1). These included: 1) north-facing mesic slopes (ELTP 42 – mesic middle slopes), and 2) south-facing dry slopes (ELTP 32 – dry upper to middle slopes). Two sample plots were then established randomly on a transect that roughly bisected the stand along the contour. The first plot was located randomly 20 to 30 m from the boundary, and the second plot was installed randomly at least 40 to 50 m from the first plot. Each sample plot consisted of a circular 500-m^2 plot and eight rectangular 1.0 m × 2.0 m quadrats. The centers of the quadrats were located 7.0 m from the center of the 500-m^2 plots in eight directions (N, NE, E, SE, S, SW, W, NW).

At the center of each plot the following physiographic features were observed or measured: aspect (azimuth in degrees), slope steepness (%), slope shape (concave, linear, or convex), length of slope, distance to nearest surface water, and the distance to the ridgetop. The percentage of the distance to the ridgetop (PDR) was calculated by dividing the distance to the ridgetop by the total length of the slope. The elevation of each plot was determined from a topographic map. Surface soil characteristics were also measured on each plot. Thickness and texture (determined by feel in the field) of the A horizon was estimated by averaging eight push-tube samples randomly located across the plot. Push-tube samples for each plot were placed in sample bags and pH of the A horizon determined in the lab using the calcium chloride method (McLean 1982).

On each 500-m^2 plot, the species, dbh (diameter at breast height; 1.37 m), and crown class (dominant, co-dominant, intermediate, and overtopped; compare Smith 1986) of all living overstory trees >10.0 cm dbh was recorded. Dead snags >10.0 cm dbh were also tallied by species and dbh on each 500-m^2 plot. Heights of the snags to the nearest meter were recorded using a clinometer. Data on the fallen trees >10.0 cm mid-diameter included species and length. Although not all snags and fallen trees were determinable to species, it was possible to determine the genus of each snag and fallen tree. Ground-flora vegetation (vascular plants <1 m tall, including pteridophytes, graminoids, forbs, woody vines, and shrubs) was sampled in each of the eight 1.0 × 2.0 m quadrats on each plot. Percent coverage was estimated visually for each ground-flora species in a quadrat using the following cover class codes: 1, <1%; 2, 1-5%; 3, 6-10%; 4, 11-20%; 5, 21-40%; 6, 41-70%; 7, 71-100%.

Data Analyses

Importance values (IV) were calculated for overstory trees as the summation of relative density and relative dominance (as expressed by basal area) divided by 2. Mean cover for each ground-flora species by plot was calculated by averaging cover class values from the eight quadrats. Mean diameter, height (m), density (stems/ha), basal area (m^2/ha) and volume (m^3/ha) of each standing dead species (snags) were computed for each plot. Similarly, the average mid-diameter, density, and volume of fallen dead stems (CWD) were also calculated.

Canonical correspondence analysis (CCA) was used to

TABLE 1

Classification of ecological landtypes (ELTs) and ecological landtype phases (ELTPs), Athens Unit, Wayne National Forest, southeastern Ohio (Goebel and Hix 1997). Old-growth ecosystems compared in this study are highlighted.

I. Level to gently sloping terrain (0-15%)
- ELT 1 Broad Level Uplands
- ELT 2 Narrow Uplands
  - *ELTP 20* Dry ridgetops; white oak-black oak/blueberry
- ELT 5 Narrow Bottomlands
  - *ELTP 50* Wet-mesic ravine bottoms; American basswood-yellow buckeye/jack-in-the-pulpit
- ELT 6 Broad Bottomlands

II. Moderately to very steeply sloping terrain (>15%)
- ELT 3 Dry Slopes with southerly aspects (136-315°)
  - *ELTP 31* Dry upper slopes; white oak/tick-trefoil
  - *ELTP 32* **Dry upper to middle slopes; white oak-chestnut oak/greenbrier**
  - *ELTP 33* Dry-mesic lower slopes; red maple-white oak/goldenrod
- ELT 4 Mesic Slopes with northerly aspects (316-135°)
  - *ELTP 41* Dry-mesic upper slopes; Northern red oak-white oak/enchanter's nightshade
  - *ELTP 42* **Mesic middle slopes; yellow buckeye-American beech/maidenhair fern**
  - *ELTP 43* Mesic middle to lower slopes; white ash-northern red oak/geranium
  - *ELTP 44* Mesic lower slopes; sugar maple/cleavers

explore the variation in species composition and site factors between the two types of old-growth ecosystem types (CANOCO; ter Braak and Smilauer 1998). Canonical correspondence analysis is an eigenvector ordination technique that provides a multivariate direct gradient analysis that helps to visualize patterns of community variation and the influence of environmental factors on species distributions (ter Braak and Smilauer 1998). CCA was performed separately on both the overstory and ground-flora datasets.

Differences in site factors and stand structure between the two types of old-growth ecosystems were measured using a Mann-Whitney test (P = 0.05). The Mann-Whitney test is a non-parametric test for two samples that does not require assumptions of normality or equal variance (Kent and Coker 1992). Mann-Whitney tests were conducted for both the overstory and ground-flora vegetation layers, as well as for the coarse woody debris.

RESULTS

Site Factors

No differences in slope percent or PDR are detected between the two old-growth ecosystems, suggesting that both are located on steeply sloping middle slopes. However, we did detect significant differences in aspect between the two old-growth ecosystems. These results confirm the classification of the individual stands into either ELTP 32 or ELTP 42 as prescribed by the Wayne National Forest ecosystem classification (Table 1). Corresponding to the different topographic positions, Mann-Whitney tests reveal that A horizon thickness and pH are significantly higher for the north-facing old-growth ecosystem compared to the south-facing old-growth ecosystem (P <0.05; Table 2).

TABLE 2

Site factors for north-facing and south-facing old-growth ecosystems in southeastern Ohio. Values are means ±1 standard error. Values in a row followed by the same letter are not significantly different at P *<0.05 (Mann-Whitney test).*

Variable	North-Facing	South-Facing
Transformed Aspect	1.72 (0.09)*a*	0.16 (0.05)*b*
Percent Slope (%)	27.4 (2.6)*a*	28.9 (2.3)*a*
Percent distance to ridgetop (PDR)	45.6 (6.0)*a*	52.3 (3.0)*a*
Thickness of A horizon (cm)	7.0 (0.9)*a*	3.5 (0.6)*b*
pH of A horizon	5.0 (0.3)*a*	3.3 (0.1)*b*

Overstory

Mixed-oaks (*Quercus* spp.) dominate the south-facing stands, while sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and northern red oak (*Quercus rubra* L.) dominate the north-facing stands (Table 3). Overstory composition accounts for 45% of the variation among old-growth ecosystems along the first two canonical axes, separating the north-facing and south-facing old-growth ecosystems along the first axis of the overstory CCA (Fig. 1). First and second axis overstory and stand-site factor correlation coefficients are very high (0.99 and 0.97, respectively); both axes combine to explain over half (55.4%) of total variation among old-growth ecosystems as explained by the site factors included in the CCA. While slope shape, PDR, and slope percent explains little of the variation among old-growth ecosystems, aspect and corresponding soil characteristics (A horizon thickness and A horizon pH) are strongly associated with the first canonical axis (Fig. 1).

Although overstory composition is different between the two old-growth ecosystems, no significant differences in stand structure are detected (P >0.05; Table 3). Basal area in the north-facing old-growth ecosystem averages (± 1 SE) 30.4 (4.2) m^2/ha, while density averages 362 (22) stems/ha. Values of basal area and density are similar for the south-facing old-growth ecosystem, averaging 30.8 (2.7) m^2/ha and 332 (25) stems/ha, respectively. Similarly, no differences in richness are detected (P >0.05) between the north-facing and south-facing stands (Table 3).

TABLE 3

Overstory importance values †, richness, basal area, and density for north-facing and south-facing old-growth ecosystems in southeastern Ohio. Values are means ±1 standard error. Values in a row followed by the same letter are not significantly different at P <0.05 (Mann-Whitney test).

Species Name	Code	Importance Value† North-Facing	Importance Value† South-Facing
Acer rubrum	ACRU	6.4 (4.3)*a*	8.8 (2.3)*a*
Acer saccharum	ACSA3	42.1 (8.5)*a*	7.5 (2.6)*a*
Aesculus flava	AEFL	9.2 (3.9)	–
Carya cordiformis	CACO15	–	0.5 (0.5)
Carya glabra	CAGL18	3.4 (1.9)*a*	0.5 (0.5)*a*
Carya ovata	CAOV2	–	0.5 (0.5)
Carya alba	CAAL	1.1 (1.1)	–
Fagus grandifolia	FAGR	8.4 (3.9)*a*	3.1 (1.6)*a*
Liriodendron tulipifera	LITU	3.2 (3.2)*a*	1.3 (1.3)*a*
Nyssa sylvatica	NYSY	0.9 (0.9)*a*	1.0 (1.0)*a*
Oxydendron arboreum	OXAR	–	0.5 (0.5)
Prunus serotina	PRSE2	2.4 (1.9)*a*	0.4 (0.4)*a*
Quercus alba	QUAL	5.4 (3.6)*a*	35.7 (7.9)*b*
Quercus coccinea	QUCO2	1.8 (1.8)*a*	1.3 (0.9)*a*
Quercus prinus	QUPR2	2.3 (2.3)*a*	23.4 (8.5)*b*
Quercus rubra	QURU	10.6 (5.3)*a*	4.8 (2.0)*a*
Quercus velutina	QUVE	–	9.4 (2.1)
Sassafras albidum	SAAL5	0.4 (0.4)*a*	0.8 (0.5)*a*
Ulmus rubra	ULRU	1.7 (l.2)	–
Structural Characteristics			
Richness (no. of species)		15*a*	16*a*
Basal area (M^2 ha^{-1})		30.4 (4.2)*a*	30.8 (2.7)*a*
Density (stems ha^{-1})		362 (22)*a*	332 (25)*a*

†Importance value = (relative dominance + relative density)/2.

Ground-flora

The characteristic ground-flora species of the north-facing old-growth ecosystem include *Actaea pachypoda* Ell., *Circaea lutetiana* L., *Osmorhiza claytoni* (Michx.) C.B. Clarke, *Viola pubescens* Ait., and *Polygonum virginianum* L., while the ground-flora of the south-facing old-growth ecosystem are dominated by *Smilax rotundifolia* L., *Solidago caesia* L., *Carex blanda* Dewey, and *Desmodium nudiflorum* (L.) DC. (Table 4). The CCA relating site factors to the ground-flora composition accounts for 33.1% of the variation among old growth stands; site factors combine to explain over 55.0% of the total variation in ground-flora composition along the first two axes. Similar to the overstory CCA, aspect and corresponding A horizon soil characteristics are strongly associated with the first canonical axis, separating the

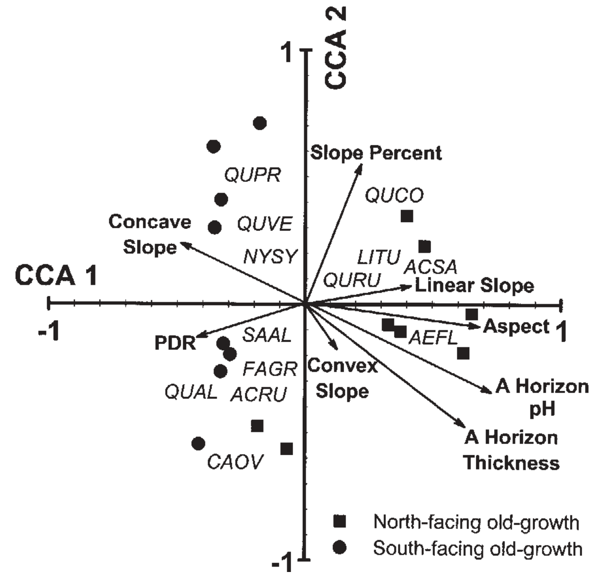

FIGURE 1. Overstory canonical correspondence analysis (CCA) triplot of old-growth ecosystems in southeastern Ohio. (See Table 3 for species acronym codes.)

north-facing and south-facing ecosystems (Fig. 2).

Mean ground-flora percent cover is not significantly different between old-growth ecosystems (*P* >0.05). Likewise, ground species richness was not significantly different between the south-facing old-growth ecosystem and the north-facing old-growth ecosystem (*P* >0.05; Table 4).

Coarse Woody Debris

Both dead snags and fallen trees differ in composition between the two old-growth ecosystems. *Acer* and *Quercus* snags dominate the north-facing ecosystem (relative densities of 56% and 28%, respectively), while only *Quercus* snags are typically observed in the south-facing ecosystem (relative density of 68%) (Table 5). Likewise, the north-facing ecosystems have high proportions of *Quercus* and *Acer* fallen trees (relative densities of 31% and 11%, respectively), while the south-facing old-growth ecosystem is comprised predominantly of *Quercus* CWD (relative density of 84%) (Table 5). Over half (57%) of the fallen trees in the north-facing old-growth ecosystem are highly decayed and unidentifiable compared to only 7% in the south-facing ecosystem type.

Fewer, larger snags are found in the north-facing old-growth ecosystem than in the south-facing ecosystem, although these differences are not significant (*P* >0.05; Fig. 3). On average (± 1 SE) the diameter at breast height of snags in the north-facing old-growth ecosystem is 32.5 (10.0) cm, while only 24.3 (4.4) cm in the south-facing old-growth ecosystem. Snag density averages 27.5 (8.4) stems/ha in the north-facing stands and 45.0 (9.0) stems/ha in the south-facing stands. Total snag volume tends to be higher in the north-facing ecosystem than the south-facing ecosystem; however, total snag volume was extremely variable (Fig. 3).

As with snag structure, the structure of fallen trees is

TABLE 4

Ground-flora mean cover values and richness for north-facing and south-facing old-growth ecosystems in southeastern Ohio. Values are means ±1 SE. Values in a row followed by the same letter are not significantly different at P *<0.05 (Mann-Whitney test).*

Species Name	Code	Mean Cover North-Facing	Mean Cover South-Facing
Actaea pachypoda	ACPA	0.23 (0.10)	–
Adiantum pedatum	ADPE	0.05 (0.05)	–
Amphicarpa bracteata	AMBR2	–	0.02 (0.02)
Antennaria plantaginifolia	ANPL	–	0.05 (0.03)
Thalictrum thalictroides	THTH2	0.05 (0.05)*a*	0.10 (0.07)*a*
Aristolochia serpentaria	ARSE3	0.02 (0.02)	–
Arisaema triphyllum	ARTR	0.02 (0.02)*a*	0.05 (0.03)*a*
Asarum canadense	ASCA	–	0.30 (0.14)
Eurybia divaricata	EUDI16	0.14 (0.09)*a*	0.53 (0.18)*a*
Eurybia macrophylla	EUMA27	0.05 (0.03)	–
Asimina triloba	ASTR	0.22 (0.22)*a*	0.13 (0.10)*a*
Botrychium virginianum	BOVI	0.09 (0.06)	–
Carex albursina	CAAL11	0.06 (0.05)	–
Carex blanda	CABL	0.03 (0.03)*a*	0.13 (0.07)*a*
Carex digitalis	CADI5	–	0.02 (0.02)
Carex gracilescens	CAGR8	0.08 (0.06)	–
Carex rosea	CARO22	0.08 (0.04)	–
Celastrus scandens	CESC	0.08 (0.05)*a*	0.02 (0.02)*a*
Chimaphila maculata	CHMA3	–	0.20 (0.16)
Circaea lutetiana	CILU	0.28 (0.11)*a*	0.05 (0.03)*b*
Cimicifuga racemosa	CIRA	0.06 (0.06)	–
Collinsonia canadensis	COCA4	0.02 (0.02)*a*	0.03 (0.03)*a*
Cunila origanoides	CUOR	–	0.05 (0.03)
Danthonia spicata	DASP2	–	0.03 (0.02)
Desmodium nudiflorum	DENU4	–	0.42 (0.23)
Disporum lanuginosum	DILA5	0.27 (0.17)	–
Eupatorium purpureum var. *purpureum*	EUPUP	–	0.14 (0.07)
Ageratina altissima var. *altissima*	AGALA	0.09 (0.04)*a*	0.06 (0.03)*a*
Festuca subverticillata	FESU3	0.13 (0.13)	–
Galium circaezans	GACI2	0.11 (0.06)*a*	0.03 (0.03)*a*
Galium concinnum	GACO3	0.30 (0.15)*a*	0.08 (0.04)*a*
Galium lanceolatum	GALA3	0.03 (0.03)*a*	0.03 (0.02)*a*
Galium triflorum	GATR3	0.03 (0.03)*a*	0.03 (0.02)*a*
Geum canadense	GECA7	0.08 (0.08)	–
Geranium maculatum	GEMA	0.28 (0.12)*a*	0.06 (0.03)*a*
Goodyera pubescens	GOPU	0.03 (0.03)*a*	0.03 (0.02)*a*
Hepatica nobilis var. *obtusa*	HENOO	0.03(0.02)	–
Hydrastis canadensis	HYCA	0.05 (0.05)	–
Lindera benzoin	LIBE3	1.02 (0.58)*a*	0.17 (0.09)*a*
Mitchella repens	MIRE	0.09 (0.07)*a*	0.02 (0.02)*a*
Monotropa uniflora	MOUN3	0.03 (0.02)*a*	0.05 (0.03)*a*
Galearis spectabilis	GASP5	0.02 (0.02)	–
Osmorhiza claytoni	OSCL	0.52 (0.19)*a*	0.11 (0.07)*a*

TABLE 4 (*Cont.*)

Ground-flora mean cover values and richness for north-facing and south-facing old-growth ecosystems in southeastern Ohio. Values are means ±1 SE. Values in a row followed by the same letter are not significantly different at P *<0.05 (Mann-Whitney test).*

Species Name	Code	Mean Cover	
		North-Facing	South-Facing
Dichanthelium boscii	DIBO2	–	0.03 (0.02)
Dichanthelium commutatum	DICO2	–	0.13 (0.09)
Dichanthelium dichotomum var. *dichotomum*	DIDID	–	0.11 (0.06)
Parthenocissus quinquefolia	PAQU2	1.08 (0.26)*a*	0.78 (0.23)*a*
Phlox divaricata	PHDI5	0.05 (0.03)*a*	0.03 (0.03)*a*
Pilea pumila	PIPU2	0.38 (0.20)*a*	0.02 (0.02)*a*
Polysticum acrostichoides	POAC4	0.28 (0.17)*a*	0.33 (0.17)*a*
Polygonatum biflorum	POBI2	0.23 (0.09)*a*	0.22 (0.06)*a*
Poa cuspidata	POCU4	0.14 (0.09)*a*	0.45 (0.14)*a*
Podophyllum peltatum	POPE	0.14 (0.09)*a*	0.05 (0.03)*a*
Potentilla simplex	POSI2	0.02 (0.02)*a*	0.33 (0.20)*a*
Porteranthus stipulatus	POST5	–	0.06 (0.06)
Polygonum virginianum	POVI2	0.25 (0.12)	–
Rosa carolina	ROCA4	–	0.14 (0.06)
Sanicula canadensis	SACA15	0.05 (0.03)*a*	0.08 (0.05)*a*
Sanicula marilandica	SAMA2	0.02 (0.02)	–
Sanicula trifoliata	SATR4	0.25 (0.13)	–
Sedum ternatum	SETE3	0.09 (0.05)*a*	0.05 (0.05)*a*
Smilax glauca	SMGL	0.02 (0.02)*a*	0.23 (0.08)*a*
Smilax tamnoides	SMTA2	0.06 (0.04)	–
Maianthemum racemosum ssp. *racemosum*	MARAR	0.20 (0.13)*a*	0.30 (0.09)*a*
Smilax rotundifolia	SMRO	–	0.80 (0.19)
Solidago caesia	SOCA4	–	0.44 (0.14)
Toxicodendron radicans	TORA2	0.22 (0.11)*a*	0.03 (0.02)*a*
Uvularia perfoliata	UVPE	0.08 (0.05)*a*	0.03 (0.03)*a*
Vaccinium pallidum	VAPA4	–	0.50 (0.27)
Viburnum acerifolium	VIAC	1.03 (0.34)*a*	1.53 (0.30)*a*
Vitis aestivalis	VIAE	0.22 (0.10)*a*	0.28 (0.12)*a*
Viola palmata	VIPA3	0.11 (0.04)*a*	0.22 (0.07)*a*
Viburnum prunifolium	VIPR	0.13 (0.10)*a*	0.05 (0.03)*a*
Viola pubescens	VIPU3	0.33 (0.20)	–
Structural Characteristics			
Total mean cover		11.2 (1.2)*a*	8.9 (1.2)*a*
Richness (no. of species)		19.6 (1.7)*a*	20.4 (1.7)*a*

highly variable between the old-growth ecosystem types. Mid-diameter of fallen trees is similar, averaging (± 1 SE) 18.5 (1.5) cm in the north-facing old-growth stands, and 17.2 (2.1) cm in the south-facing old-growth stands (*P* >0.05). Whereas snag density tends to be higher in the south-facing old-growth ecosystem, fallen tree density tends to be higher in the north-facing ecosystem (*P* <0.10). Volume of fallen trees is also significantly different (*P* <0.05), with higher volumes in the north-facing stands than the south-facing stands (Fig. 4).

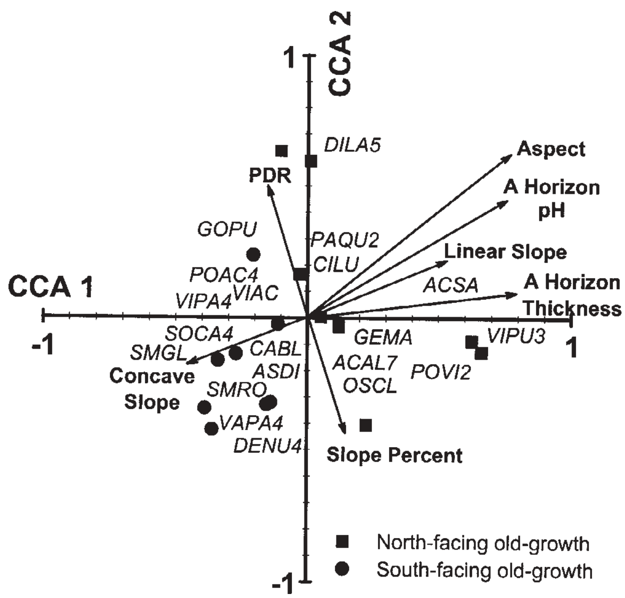

FIGURE 2. Ground-flora canonical correspondence analysis (CCA) triplot of old-growth ecosystems in southeastern Ohio. (See Table 4 for species acronym codes.)

DISCUSSION

Most studies of old-growth forests in eastern North America have focused on individual tracts instead of taking an ecosystem approach to characterize the composition and structure of old-growth forest ecosystem types (for example, Roovers and Shifley 1997). As a result, our knowledge and understanding of the composition, structure, and function of eastern old-growth has primarily been obtained by studying old-growth remnants. Furthermore, the composition and structure of current second-growth stands have been compared to those of remnant old-growth stands to determine the successional status of the second-growth stands (Hale and others 1999), as well as guiding any forest management practices designed to emulate old-growth conditions. This can be problematic for forest ecosystem restoration as these individual old-growth remnants are often used as 'blueprints' for restoration (Frelich and Puettmann 1999), and do not adequately represent the inherent variability in these forest ecosystems. Consequently, research that is focused on developing reference conditions for forest ecosystem restoration should focus on developing composite descriptions based on measurements taken from several locations rather than a single site or old-growth remnant (SER 2002). Our landscape ecosystem approach provides us with such an opportunity to develop a suite of composite reference conditions for old-growth ecosystem types. Additionally, our utilization of the Wayne National Forest ecosystem classification system (which was based on mature second-growth forests) provides us with a framework with which to compare the ecological properties of these contrasting old-growth ecosystem types rather than merely summarizing the characteristics of a single stand of old trees or old-growth remnant.

In southeastern Ohio, the stand structure is relatively similar between north-facing and south-facing old-growth forest ecosystem types. Our results suggest that these forest ecosystem types have 15 to 16 different overstory species, approximately 30 m^2/ha of basal area, and densities between 322 and 360 trees/ha. However, the old-growth north-facing middle slope ecosystem types are dominated by overstories of mesic species, including sugar maple, northern red oak, and American beech while old-growth south-facing ecosystem types are dominated by mixed-oaks. Similar trends, that is, different composition but similar structure, are also observed with the coarse woody debris in these ecosystem types. However, there appears to be considerable variability in the coarse woody debris both within and between ecosystem types.

Corresponding to differences in A-horizon characteristics, the ground-flora composition of the old-growth ecosystem type located on north-facing slopes is dominated by a rich community of mesic perennials, including *Actaea pachypoda* Ell., *Circaea lutetiana* L., *Osmorhiza claytoni* (Michx.) C.B. Clarke, *Viola pubescens* Ait., and *Polygonum virginianum* L. Different species, including *Smilax rotundifolia* L., *Solidago caesia* L., *Carex blanda* Dewey, and *Desmodium nudiflorum* (L.) DC., characterize the south-facing old-growth ecosystem type. These species include a mixture of xeric woody vines and shrubs, perennials, and graminoids. Contrary to what we would have anticipated based on the edaphic difference observed between these two forest ecosystem types, ground-flora species richness and total cover are similar.

As demonstrated here, quantifying the differences in composition and structure of different old-growth ecosystem types rather than individual old-growth remnants is the first step in effectively managing the remaining and future old-growth forests of the Central Hardwoods Region (Sauer 1998). By focusing on the interrelationships between local ecosystem components,

TABLE 5

Relative density of coarse woody debris (CWD) between south-facing and north-facing old-growth ecosystems of southeastern Ohio.

Genus	North-facing	South-facing
Standing Snags		
Quercus	28.0	68.0
Carya	8.0	11.0
Acer	56.0	5.0
Fagus	0.0	5.0
Other	8.0	11.0
Fallen Trees		
Quercus	31.0	84.0
Carya	1.0	2.0
Acer	11.0	7.0
Fagus	0.0	0.0
Other	57.0	7.0

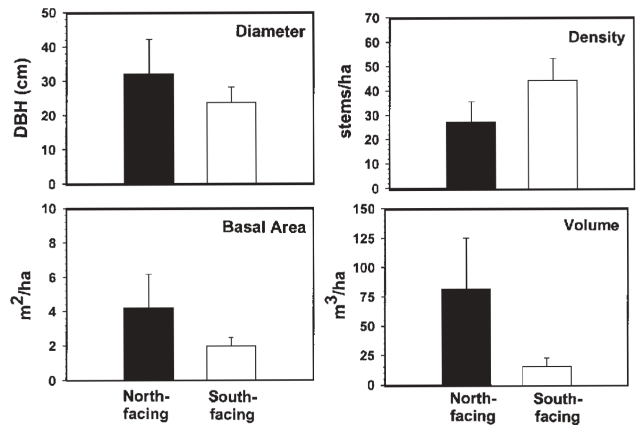

FIGURE 3. Snag characteristics of north-facing and south-facing old-growth ecosystems in southeastern Ohio.

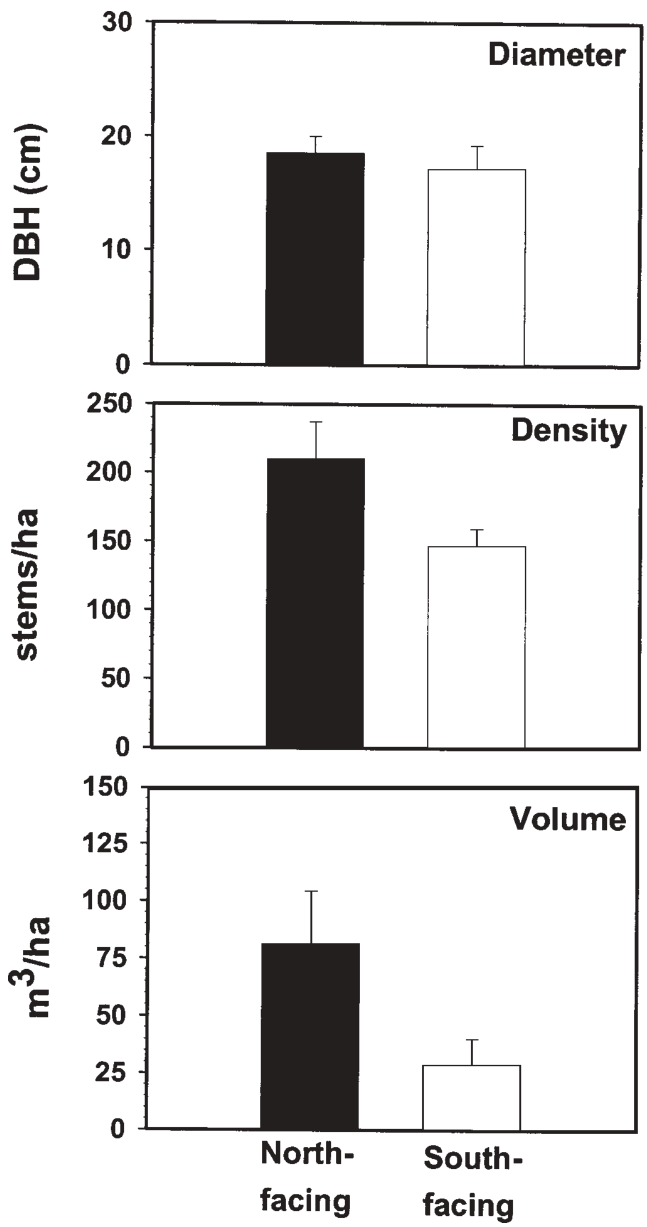

FIGURE 4. Coarse woody debris (CWD) characteristics of north-facing and south-facing old-growth ecosystems in southeastern Ohio.

such as the influence of physiography and soils on the composition and structure of old-growth plant communities, a better understanding of the old-growth processes will surely follow. Additionally, we can begin to quantify the variation in different compositional and structural components of these forest ecosystem types, an important first-step in forest ecosystem restoration (Palmer and others 1997), as well as develop management practices that emulate the natural disturbance regimes that influence the composition and structure of forest ecosystems (Palik and others 2002). The end result will lead to the improvement of functional definitions of eastern old-growth forest ecosystems, and ultimately advance our ability to effectively restore and manage them.

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