Tree regeneration ecology of an old-growth central Appalachian forest: Diversity, temporal dynamics, and disturbance response

Author(s): Julia I. Chapman and  Ryan W. McEwan

# Tree regeneration ecology of an old-growth central Appalachian forest: Diversity, temporal dynamics, and disturbance response[1,2]

### Julia I. Chapman and Ryan W. McEwan[3]

Department of Biology, University of Dayton, Dayton, OH 45469

CHAPMAN, J. I. AND R. W. MCEWAN (Department of Biology, University of Dayton, Dayton, OH 45469). Tree regeneration ecology of an old-growth central Appalachian forest: Diversity, temporal dynamics, and disturbance response. J. Torrey Bot. Soc. 139: 194–205. 2012.—Diversity and compositional dynamics in deciduous forests of eastern North America are subject to an array of drivers, and these forests are thought to be undergoing a long-term dominance shift in which maples (*Acer* spp.) are replacing oaks (*Quercus* spp.). We examined dynamics of woody understory species in an old-growth central Appalachian forest to document baseline dynamics over a decade and describe the relationships between diversity and surrogate measures of productivity (density and cover). We also investigated the reaction of shrub- and ground-layer vegetation to a recent fire in one portion of the study site. Over a ten-year interval (2000–2010), shrub-layer densities of *Acer* spp. decreased significantly ($P < 0.01$) and *Quercus* spp. did not change. Ground-layer densities of *Acer* spp. increased significantly ($P < 0.01$) while mean cover decreased significantly ($P < 0.01$). For a few *Quercus* species, ground-layer densities increased significantly ($P < 0.01$), and mean cover of ground-layer *Quercus alba* increased significantly ($P < 0.05$). Significant unimodal relationships ($P < 0.01$) were exhibited between diversity/richness and density/cover in both understory strata. Plots burned by a wildfire in 2010 had significantly lower shrub-layer density and species richness ($P < 0.01$) compared to pre-disturbance data in 2000. In the same area, the ground-layer response to this fire disturbance was equivocal, with increased density, decreased cover, and unchanged diversity and richness. Decadal oak-maple dynamics in the woody understory of this old-growth stand did not fully support the hypothesized oak-to-maple dominance shift; changes in shrub- and ground-layer populations of *Acer* spp. were erratic while *Quercus* spp. populations appeared stable. Unimodal relationships between diversity and productivity surrogates were found in both woody understory layers and are likely driven by the range of environmental conditions found within the study site. Fire induced short-term changes in the shrub- and ground-layers and may have facilitated colonization of invasive species. Quantification of changes across all woody forest strata in areas of minimal anthropogenic disturbance (e.g., old-growth stands) is important for understanding baseline dynamics of deciduous forests in eastern North America.

Key words: Appalachian, diversity, ground-layer, old-growth, shrub-layer.

Diversity and compositional dynamics in deciduous forests of eastern North America are subject to an array of drivers. Natural ecosystem drivers include small-scale disturbances that create canopy gaps (Runkle 1982) and large-scale disturbance events, such as windthrow events and ice storms (Turner et al.

1998). Pathogens and insect pests can alter forest composition by severely reducing the abundance of particular species, as exemplified by the loss of American chestnut (*Castanea dentata* (Marsh.) Borkh) due to the chestnut blight that moved through the Appalachian Mountains ca. 1950 (McCormick and Platt 1980). A variety of anthropogenic influences, such as timber harvesting, agriculture, and altered fire regimes, also play a role in determining the successional trajectories of eastern deciduous forests (Christensen 1989, Shumway et al. 2001, McEwan et al. 2011).

Forests across eastern North America are undergoing an important shift in species composition as oaks (*Quercus* spp.) are being replaced by mesophytic species (Nowacki and Abrams 2008), especially maples (*Acer* spp.; Lorimer 1984, Host et al. 1987, Crow 1988, Shotola et al. 1992, Abrams 1998). This shift in dominance, thought to be the result of altered disturbance regimes (Arthur et al. 1998, Albrecht and McCarthy 2006), is predicted to have important ecological and

economic impacts (Alexander and Arthur 2010, Knoot et al. 2010). One challenge of documenting forest dynamics is that dominance patterns in understory layers at one point in time are not necessarily indicative of long-term understory composition, or the future of the forest overstory, due to low survivorship of seedling and sapling populations (Boerner and Brinkman 1996). While many studies offer evidence of an oak-to-maple shift (Lorimer 1984, Parker et al. 1985, Host et al. 1987, Crow 1988, Pallardy et al. 1988, McEwan and Muller 2006), continued long-term quantification of changes across all woody strata is needed to fully understand the implications of this successional trajectory.

Compositional shifts have the potential to influence forest understory species diversity, which is known to be regulated by disturbance and resource gradients. A unimodal relationship between diversity and productivity has been proposed as a general theory of plant community diversity (Al-Mufti et al. 1977, Grime 1979, Huston 1979, Grace 1999). This theory proposes that diversity is constrained at the lowest levels of productivity by environmental stress and at the highest levels of productivity by competition (Huston 1979). Although the broader applicability of this concept has been questioned (Oksanen 1996, Rapson et al. 1997, Liira and Zobel 2000, Chase and Leibold 2002), this relationship has been described in a variety of habitats (Grace 1999, Fornara and Tilman 2009). The presence of this unimodal diversity-productivity relationship as a general pattern in forest understories has not been scientifically established.

An old-growth Appalachian forest in southeastern Kentucky provided a unique opportunity to assess forest regeneration dynamics and diversity-productivity relationships. This particular stand has a rich research history beginning in the early 1970s, and the woody understory was sampled in 2000, providing an opportunity for resampling (McEwan et al. 2005a). The site has been carefully protected; however, a wildfire recently impacted some parts of the study area, providing an opportunity to study initial fire responses in an old-growth forest. Our goal was to describe temporal dynamics of the woody understory and explore diversity-productivity relationships. Our hypotheses were (i) a shift in dominance from oak to maple would be seen over a ten-year period; that (ii) diversity would exhibit a significant unimodal relationship to productivity; and (iii) diversity and productivity of an area that experienced fire in 2010 would differ significantly from pre-disturbance data from 2000. This study also served to establish baseline data for continued monitoring of long-term responses to fire and invasive plant species arrival, as well as the ecological response to the recent invasion of the hemlock woolly adelgid (*Adelges tsugae* Annand).

**Materials and Methods.** STUDY AREA. Big Everidge Hollow (BEH) is a 52 ha watershed located within the Lilley Cornett Woods Appalachian Research Station on the Cumberland Plateau in eastern Kentucky (37° 05′ N, 83° 00′ W, Roxana Quadrangle). This tract of land is near the geographic center of the mixed mesophytic forest region described by Braun (1950). The regional climate is temperate humid continental with warm summers, cool winters, and no distinct dry season (Trewartha 1968). Mean annual precipitation and temperature are 133 cm and 13°C, respectively (Hill 1976). Soils are mostly loam and silt-loam, and rock outcrops are common (Martin 1975).

The BEH watershed has no history of timber harvest, although some downed American chestnut (*Castanea dentata*) logs were salvaged following the blight. There has also been some minimal disturbance from trespassers collecting medicinal herbs and from hog grazing on a small portion of the upper north-facing slope in the early 1900s. Big Everidge Hollow had no known history of fire within the recent past until the spring of 2010, when an arson fire set in an adjacent stand of second-growth forest burned through parts of the upper south- and east-facing slopes. Prior to this study, no invasive species had been reported within the BEH old-growth watershed (McEwan et al. 2005b).

DATA COLLECTION. Eighty permanent overstory plots were established by Muller (1982) in 1979, each covering a circular 0.04 ha area. The plots were laid out according to a stratified random sampling design. The north-facing and south-facing slopes were divided into three elevation strata (upper, middle, and lower), and the east-facing slope was divided into upper and middle strata. A lower sampling stratum was not possible on the east-facing slope due to the topography of this "u-shaped" watershed. The BEH watershed

opens to the east, so a west-facing slope does not exist. Muller (1982) identified three over-story community types within the watershed that were used to group plots for statistical analyses: Beech ($n = 31$), Mixed mesophytic ($n = 17$), and Chestnut oak ($n = 32$).

Four subplots were established by McEwan et al. (2000) within each overstory plot, for a total of 320 subplots throughout the water-shed. The subplot centers were spaced 90° around the overstory plot center at a radius bisecting the overstory plot area, with the first subplot 45° uphill to the right. The subplots consist of nested sampling areas, with a smaller 1 m² (0.0001 ha) circular plot centered inside a larger 10 m² (0.001 ha) circular plot. All woody stems in the subplots were previ-ously sampled in 2000 (McEwan et al. 2005a).

The shrub- and ground-layers were resam-pled following the same protocol used by McEwan et al. (2005a) in the original 2000 sampling. The shrub-layer was inventoried within the 10 m² subplots and included all woody stems > 50 cm in height but < 2.5 cm in diameter at breast height (DBH). The ground-layer was inventoried within the 1 m² subplots and included all woody stems < 50 cm in height. Density was recorded for shrub- and ground-layer species. Percent vegetation cover of each ground-layer species was estimated using a modified Domin scale (McCune and Grace 2002): < 1%, 1–5%, 6–10%, 11–25%, 26–35%, 36–50%, 51–75%, 76–90%, 91–100%. Botanical nomenclature followed Jones (2005).

DATA ANALYSIS. Relative importance values (RIV) were used to rank species within each layer. Shrub-layer RIVs were the mean of relative density (density of a species/Σ densities of all species) and relative frequency (frequen-cy of a species/Σ frequencies of all species) values for each species. Ground-layer RIVs were the mean of relative density, relative cover, and relative frequency values for each species. Minor species were those with an RIV less than one.

Within each overstory plot, data collected within the four subplots were pooled ($n = 80$) and used to calculate mean density (stems ha$^{-1}$) and cover. Median values of percent cover classes were converted to cover values (cm² m$^{-2}$). Shannon-Wiener diversity ($H' = -\Sigma p_i \ln p_i$, where $p_i$ is the proportion of stems of the $i$th species), species richness ($S = \#$

species in a plot), and evenness ($E = H'/\ln(S)$) were calculated for each plot (McCune and Grace 2002). Linear and quadratic regressions were used to analyze relationships between measures of diversity (S, H', E) and produc-tivity surrogates (mean cover and mean density), and fits were evaluated via assess-ment of $r^2$ and $P$-values. Cover and density were used as non-destructive, surrogate mea-surements of productivity, as they have been shown to correlate positively with biomass, another commonly used measurement of pro-ductivity (Gilliam and Turrill 1993, Bergamini et al. 2001).

Select species were analyzed for significant changes in mean density and mean cover over a ten-year span. Oaks (*Quercus alba* L., *Q. coccinea* Münchh., *Q. montana* Willd., *Q. rubra* L., *Q. velutina* Lam.) and maples (*Acer rubrum* L. and *A. saccharum* Marsh.) were of primary interest because of their roles in the hypothesized oak-to-maple shift in eastern deciduous forests (Nowacki and Abrams 2008). *Fagus grandifolia* Ehrh., *Fraxinus amer-icana* L., *Sassafras albidum* (Nutt.) Nees., and *Nyssa sylvatica* Marsh., all of which are commonly found among the canopy or sub-canopy, were included as well. *Cornus florida* L. and *Tsuga canadensis* (L.) Carr. were included to detect changes associated with dogwood anthracnose infection and hemlock wooly adelgid infestation, respectively. Dy-namics of ground-layer *Liriodendron tulipifera* L. were examined, due to its capacity to respond to fire (Albrecht and McCarthy 2006). Shapiro-Wilk normality tests indicated non-normality of density and cover measure-ment distributions for all species considered; therefore, paired Wilcoxon rank-sum tests were used to compare density and cover between 2000 and 2010 for each of the selected species.

Additional analyses were performed to identify initial fire responses. Of the 32 oak community type plots (Muller 1982), 20 were burned in the spring 2010 fire and served as fire treatment plots—the remaining 12 plots were undisturbed and served as "control" plots. Previously collected data from 2000 served as pre-disturbance data. Measures of diversity (S, H', E) and productivity (mean cover, mean density) for each group of plots (control and burned) were compared between 2010 and 2000 using paired Wilcoxon rank-sum tests (not all groups of measurements

Table 1. Mean density (stems ha$^{-1}$), relative density (%), frequency (percentage of plots on which a species occurred), relative frequency (%), and relative importance values (RIV) of shrub-layer species in 2010. Species are rank ordered based on RIV, where RIV = (relative density + relative frequency)/2.

| | Mean density | Relative density | Frequency | Relative frequency | RIV |
|---|---|---|---|---|---|
| Smilax rotundifolia | 887.5 | 19.4 | 73.8 | 13.2 | 16.3 |
| Fagus grandifolia | 571.9 | 12.5 | 55.0 | 9.8 | 11.2 |
| Acer saccharum | 396.9 | 8.7 | 53.8 | 9.6 | 9.1 |
| Acer rubrum | 331.3 | 7.2 | 38.8 | 6.9 | 7.1 |
| Amelanchier arborea | 203.1 | 4.4 | 35.0 | 6.3 | 5.3 |
| Lindera benzoin | 368.8 | 8.1 | 13.8 | 2.5 | 5.3 |
| Asimina triloba | 246.9 | 5.4 | 20.0 | 3.6 | 4.5 |
| Fraxinus americana | 159.4 | 3.5 | 28.8 | 5.1 | 4.3 |
| Kalmia latifolia | 265.6 | 5.8 | 10.0 | 1.8 | 3.8 |
| Quercus montana | 184.4 | 4.0 | 11.3 | 2.0 | 3.0 |
| Oxydendrum arboreum | 93.8 | 2.1 | 17.5 | 3.1 | 2.6 |
| Vaccinium stamineum | 96.9 | 2.1 | 7.5 | 1.3 | 1.7 |
| Cornus florida | 46.9 | 1.0 | 12.5 | 2.2 | 1.6 |
| Magnolia macrophylla | 50.0 | 1.1 | 11.3 | 2.0 | 1.6 |
| Aesculus flava | 37.5 | 0.8 | 11.3 | 2.0 | 1.4 |
| Liriodendron tulipifera | 75.0 | 1.6 | 6.3 | 1.1 | 1.4 |
| Nyssa sylvatica | 37.5 | 0.8 | 8.8 | 1.6 | 1.2 |
| Quercus velutina | 37.5 | 0.8 | 8.8 | 1.6 | 1.2 |
| Smilax glauca | 34.4 | 0.8 | 8.8 | 1.6 | 1.2 |
| Carya cordiformis | 28.1 | 0.6 | 8.8 | 1.6 | 1.1 |
| Quercus rubra | 25.0 | 0.5 | 8.8 | 1.6 | 1.1 |
| Tilia americana | 25.0 | 0.5 | 8.8 | 1.61 | 1.1 |
| Minor Species* | 368.8 | 8.1 | na | 18.1 | 13.1 |
| Totals | 4571.9 | 100 | na | 100 | 100 |

* Minor species: Hydrangea arborescens, Vitis sp., Tsuga canadensis, Carya tomentosa, Ostrya virginiana, Quercus alba, Carya glabra, Ulmus rubra, Vaccinium corymbosum, Cercis canadensis, Pyrularia pubera, Sassafras albidum, Hamemelis virginiana, Rhododendron cumberlandense, Viburnum acerifolium, Dioscorea quaternata, Euonymus americanus, Aristolochia macrophylla, Betula lenta, Castanea dentata, Quercus coccinea, Ulmus americana, Vaccinium pallidum, Acer pennsylvanicum, Juglans nigra, Juniperus virginiana, Magnolia acuminata, Morus rubra, Parthenocissus quinquefolia, Pinus echinata, Prunus serotina, Robinia pseudoacacia, Rosa multiflora, Smilax hispida.

were normally distributed). Control and burned groups were also compared within years using Mann-Whitney tests. The multi-response permutation procedure (MRPP) was used to test for differences in shrub- and ground-layer species composition. For this analysis, presence/absence data were used with rare species removed (those occurring on less than two plots). We tested for differences between pre-fire (2000) and post-fire (2010) samplings and between control and burned areas within each year. All statistical procedures were performed using R version 2.11.1 (R Core Development Team 2010).

**Results. Woody Understory Dynamics.** Across the watershed in 2010, 56 species were found in the shrub-layer (Table 1) and 59 species were found in the ground-layer (Table 2). The shrub-layer was dominated by Smilax rotundifolia L., which had the highest relative density and relative frequency. Acer saccharum and A. rubrum were among the top five most important species in both understory strata with the latter dominating the ground-layer (Table 2). The most important oak species for both strata was Quercus montana (Table 1, 2). Fagus grandifolia, Liriodendron tulipifera, and Fraxinus americana were important in both understory layers as well (Table 1, 2). Two invasive species were found during this sampling (Ailanthus altissima (Mill.) Swingle and Rosa multiflora Thunb.). A third invasive species (Paulownia tomentosa (Thunb.) Siebold & Zucc. ex Steud.) was also noted but did not fall within the sampling area.

Significant decreases in mean density over ten years were observed for several species in the shrub-layer (Fig. 1). Mean densities of shrub-layer Acer rubrum and Acer saccharum decreased significantly ($P < 0.01$) over the ten-year span (Fig. 1). Cornus florida, Nyssa sylvatica, and Sassafras albidum also had significantly lower shrub-layer densities ($P < 0.01$) in 2010 compared to 2000 (Fig. 1). Though not significant, three of the five

Table 2.   Mean cover (cm$^2$ m$^{-2}$), relative cover (%), mean density (stems ha$^{-1}$), relative density (%), frequency (percentage of plots on which a species occurred), relative frequency (%), and relative importance values (RIV) of ground-layer species in 2010. Species are rank ordered based on RIV, where RIV = (relative cover + relative density + relative frequency)/3.

| | Mean cover | Relative cover | Mean density | Relative density | Frequency | Relative frequency | RIV |
|---|---|---|---|---|---|---|---|
| Acer rubrum | 63.4 | 14.8 | 44718.75 | 30.2 | 95.0 | 10.2 | 18.4 |
| Fraxinus americana | 25.3 | 5.9 | 18843.75 | 12.7 | 48.8 | 5.2 | 8.0 |
| Liriodendron tulipifera | 18.1 | 4.2 | 17593.75 | 11.9 | 60.0 | 6.5 | 7.5 |
| Smilax rotundifolia | 38.6 | 9.0 | 7812.5 | 5.3 | 68.8 | 7.4 | 7.2 |
| Acer saccharum | 25.0 | 5.8 | 7656.25 | 5.2 | 53.8 | 5.8 | 5.6 |
| Parthenocissus quinquefolia | 21.6 | 5.0 | 5031.25 | 3.4 | 63.8 | 6.9 | 5.1 |
| Vitis sp. | 11.4 | 2.7 | 4781.25 | 3.2 | 48.8 | 5.2 | 3.7 |
| Amelanchier arborea | 17.2 | 4.0 | 4531.25 | 3.1 | 30.0 | 3.2 | 3.4 |
| Quercus montana | 20.2 | 4.7 | 2781.25 | 1.9 | 31.3 | 3.4 | 3.3 |
| Vaccinium pallidum | 12.8 | 3.0 | 6593.75 | 4.5 | 15.0 | 1.6 | 3.0 |
| Fagus grandifolia | 18.9 | 4.4 | 812.5 | 0.5 | 25.0 | 2.7 | 2.6 |
| Kalmia latifolia | 15.2 | 3.5 | 2031.25 | 1.4 | 8.8 | 0.9 | 2.0 |
| Sassafras albidum | 6.9 | 1.6 | 2156.25 | 1.5 | 23.8 | 2.6 | 1.9 |
| Toxicodendron radicans | 4.7 | 1.1 | 2000 | 1.4 | 28.8 | 3.1 | 1.8 |
| Quercus alba | 8.0 | 1.9 | 1375 | 0.9 | 20.0 | 2.2 | 1.6 |
| Nyssa sylvatica | 5.2 | 1.2 | 1125 | 0.8 | 25.0 | 2.7 | 1.6 |
| Euonymus americanus | 3.3 | 0.8 | 2593.75 | 1.8 | 17.5 | 1.9 | 1.5 |
| Smilax glauca | 4.2 | 1.0 | 1187.5 | 0.8 | 22.5 | 2.4 | 1.4 |
| Rhododendron cumberlandense | 9.1 | 2.1 | 1281.25 | 0.9 | 10.0 | 1.1 | 1.4 |
| Magnolia macrophylla | 10.3 | 2.4 | 593.75 | 0.4 | 11.3 | 1.2 | 1.3 |
| Bignonia capreolata | 3.4 | 0.8 | 2187.5 | 1.5 | 10.0 | 1.1 | 1.1 |
| Rubus sp. | 7.7 | 1.8 | 687.5 | 0.5 | 10.0 | 1.1 | 1.1 |
| Lindera benzoin | 6.9 | 1.6 | 500 | 0.3 | 10.0 | 1.1 | 1.0 |
| Tilia americana | 3.4 | 0.8 | 656.25 | 0.4 | 15.0 | 1.6 | 1.0 |
| Minor Species* | 67.5 | 15.8 | 8343.75 | 5.6 | na | 19.1 | 13.5 |
| Column Totals | 428.1 | 100 | 147875 | 100 | na | 100 | 100 |

* Minor Species: *Asimina triloba, Dioscorea quaternata, Oxydendrum arboreum, Pyrularia pubera, Quercus velutina, Cornus florida, Cercis canadensis, Hamamelis virginiana, Robinia pseudoacacia, Chimaphila maculata, Magnolia acuminata, Vaccinium stamineum, Carya glabra, Quercus rubra, Carya cordiformis, Prunus serotina, Ulmus rubra, Smilax hispida, Vaccinium corymbosum, Rhus glabra, Quercus coccinea, Aristolochia macrophylla, Aesculus flava, Carya tomentosa, Ostrya virginiana, Viburnum acerifolium, Rosa carolina, Ailanthus altissima, Hydrangea arborescens, Juniperus virginiana, Pinus echinata, Quercus muhlenbergii, Rosa multiflora, Tsuga canadensis, Magnolia tripetala.*

*Quercus* species showed slight increases in mean shrub-layer density over ten years (Fig. 1).

There was clear evidence of decadal change in density and cover of some species in the ground-layer. *Acer rubrum* and *Acer saccharum* both decreased significantly in mean cover ($P < 0.01$) but increased in mean density ($P < 0.01$; Fig. 2). *Fraxinus americana* exhibited a significant increase in density ($P < 0.01$) over the sampling interval, and *Liriodendron tulipifera* increased in both density and cover ($P < 0.01$; Fig 2). Mean ground-layer densities of *Quercus montana* ($P < 0.05$), *Quercus alba* ($P < 0.01$), and *Quercus velutina* ($P < 0.01$) increased (Fig. 2). The only oak species that showed a significant change in mean cover over the ten-year interval was *Q. alba* with an increase ($P < 0.05$).

Diversity and richness varied predictably across gradients of stem density and cover in both the shrub- and ground-layers (Fig. 3). Shrub-layer stem density exhibited highly significant unimodal relationships with both diversity ($r^2 = 0.28$, $P < 0.001$) and species richness ($r^2 = 0.45$, $P < 0.001$; left column, Fig. 3). Polynomial models of shrub-layer diversity-density and richness-density relationships had greater explanatory power than linear models ($r^2 = 0.13$ and $r^2 = 0.39$, respectively). Neither linear nor polynomial models were significant for explaining the relationship between evenness and shrub-layer stem density (data not shown).

Similar relationships were evident in the ground-layer, where diversity and richness varied predictably with density and cover (Fig. 3). Ground-layer density exhibited a significant unimodal relationship with richness ($r^2 = 0.33$, $P < 0.001$), but not diversity ($P = 0.08$; middle column, Fig. 3). Ground-layer
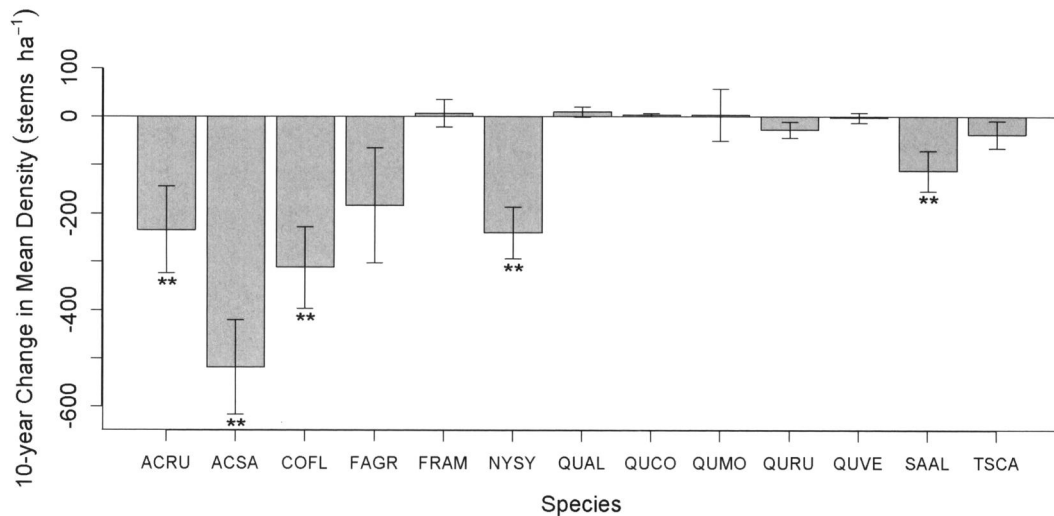
FIG. 1. Ten-year shifts (2000–2010) in density (stems ha$^{-1}$) of selected shrub-layer species in the Big Everidge Hollow watershed. Bars represent the change in mean density over a ten-year sampling interval. Species are listed in alphabetical order by the first two letters of the genus and specific epithet. Statistical significance: * $P < 0.05$; ** $P < 0.01$.

cover had significant unimodal relationships with diversity ($r^2 = 0.11$, $P < 0.01$) and richness ($r^2 = 0.29$, $P < 0.001$; right column, Fig. 3). All three of these significant polynomial models had greater explanatory power than corresponding linear models ($r^2 = 0.26$, $r^2 = 0.09$, and $r^2 = 0.24$). Both linear and polynomial models were significant for explaining the relationship between evenness and ground-layer density ($P < 0.01$), and the explanatory power of these relationships was similar ($r^2 = 0.15$ and $r^2 = 0.14$, respectively; data not shown).

FIRE RESPONSE. Density, richness, and diversity of the shrub-layer responded variably to the May 2010 fire within oak community plots (Fig. 4). Prior to the fire (first column, Fig. 4), there were no statistical differences in stem density between the plots that were later burned (filled circles) and those that were not (open circles; Fig. 4). Mean density of the control plots (open circles) did not change significantly over the ten-year interval, but the mean density of the burned plots (filled circles, second column, Fig. 4) decreased significantly compared to pre-disturbance data ($P < 0.001$). Mean richness was similar between the two groups of plots in 2000, but after the fire, the burned group of plots had significantly lower richness than the control plots ($P < 0.01$; filled circles, top row, Fig. 4). The difference in mean diversity between the two groups of

plots was marginally significant ($P = 0.045$) in 2000, but was more pronounced in 2010 ($P < 0.01$; bottom row, Fig. 4).

Prior to the fire disturbance in 2000, shrub-layer density did not exhibit significant relationships with richness or diversity within the oak community plots (first column, Fig. 4). After the 2010 fire, richness-density and diversity-density relationships in the shrub-layer could both be described by significant linear relationships ($P < 0.01$) with considerable explanatory power ($r^2 = 0.49$ and $r^2 = 0.26$ respectively; second column, Fig. 4). The burn in 2010 affected ground-layer density (increased, $P < 0.001$) and cover (decreased, $P < 0.001$); however, diversity and richness were similar between the burned and control plots, and diversity-productivity relationships were consistent over time (data not shown).

The MRPP analysis indicated that the 2010 wildfire altered the composition of the woody understory. Within either sampling year (2000 or 2010), shrub- and ground-layer species composition did not differ significantly between the burned and control plots ($P > 0.1$). Comparison of pre-fire (2000) and post-fire (2010) data revealed that in the control area, shrub- and ground-layer species composition did not differ over time ($P > 0.2$). In the burned area, however, both layers changed significantly in their composition over ten years ($P < 0.001$).
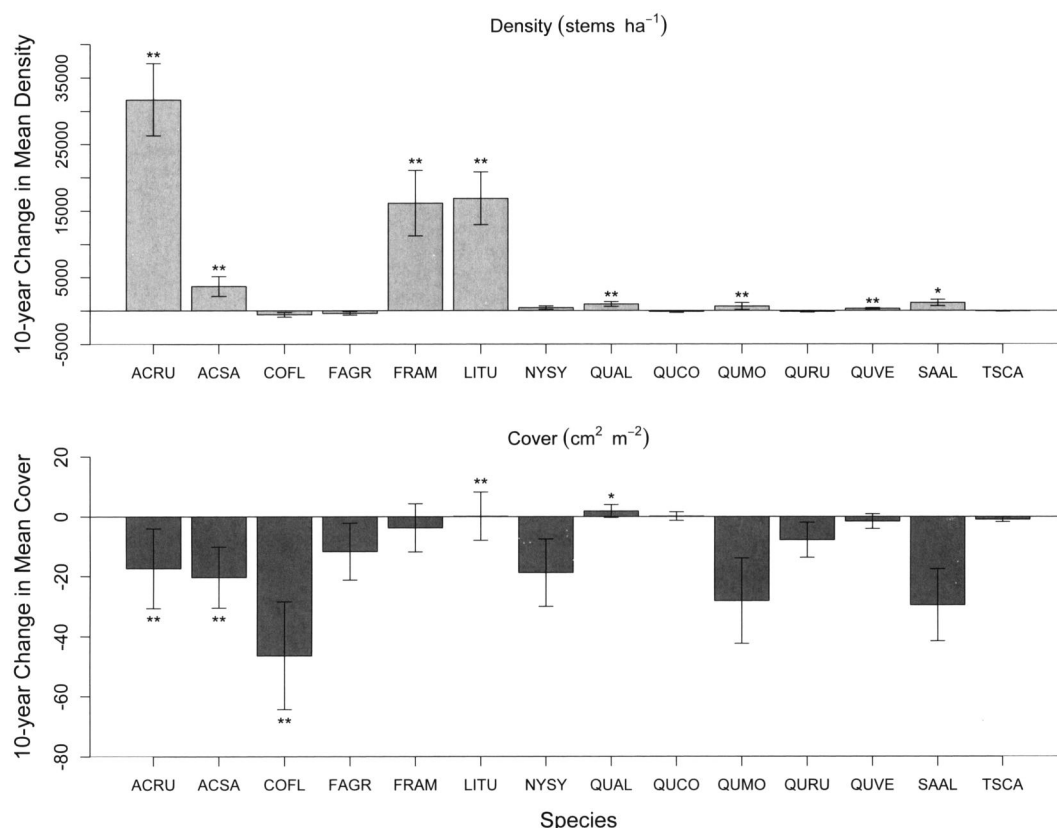
FIG. 2. Ten-year shifts (2000–2010) in density and cover of selected ground-layer species in the Big Everidge Hollow watershed. Bars represent the changes in mean density (stems ha$^{-1}$) and mean cover (cm$^2$ m$^{-2}$) over a ten-year sampling interval. Species are listed in alphabetical order by the first two letters of the genus and specific epithet. Statistical significance: * $P < 0.05$; ** $P < 0.01$.

**Discussion.** A dominance shift from oaks to mesophytic species is thought to be ongoing across the eastern deciduous forests of North America (Abrams 1998, Nowacki and Abrams 2008, McEwan et al. 2011). The regeneration layers of modern eastern deciduous forests have been noted for a paucity of oaks (Lorimer 1984, Crow 1988, Boerner and Brinkman 1996, Goebel and Hix 1996, Arthur et al. 1998, Hutchinson et al. 2005, McEwan et al. 2005a), and increased importance of mesophytic species, especially *Acer* spp. (Lorimer 1984, Parker et al. 1985, Host et al. 1987, Pallardy et al. 1988, Shotola et al. 1992, Abrams 1998). Analyses of presettlement witness tree data also provide evidence of significant compositional changes over the past two centuries (Fralish et al. 1991, Abrams and Ruffner 1995, Dyer 2001). While the underlying drivers are not fully understood (McEwan et al. 2011), the expected outcome

is "mesophication" of forests (Nowacki and Abrams 2008), where a more mesic, shaded understory environment results from the denser canopy of increasingly dominant mesophytic species.

Previous studies of BEH suggested a shift toward mesophytic species dominance in the overstory and midstory (McEwan and Muller 2006) and described an abundance of maple in the woody understory (McEwan et al. 2005a); thus, we hypothesized that an oak-to-maple dominance shift would be prevalent in the woody understory of the watershed. The regeneration trends seen over a ten-year sampling interval in the BEH watershed did not fully support our hypothesis. While ground-layer *Acer* species increased in density, shrub-layer abundance decreased over the ten-year interval. *Quercus* species were expected to show significant decreases in cover and density over the ten-year interval, but variations
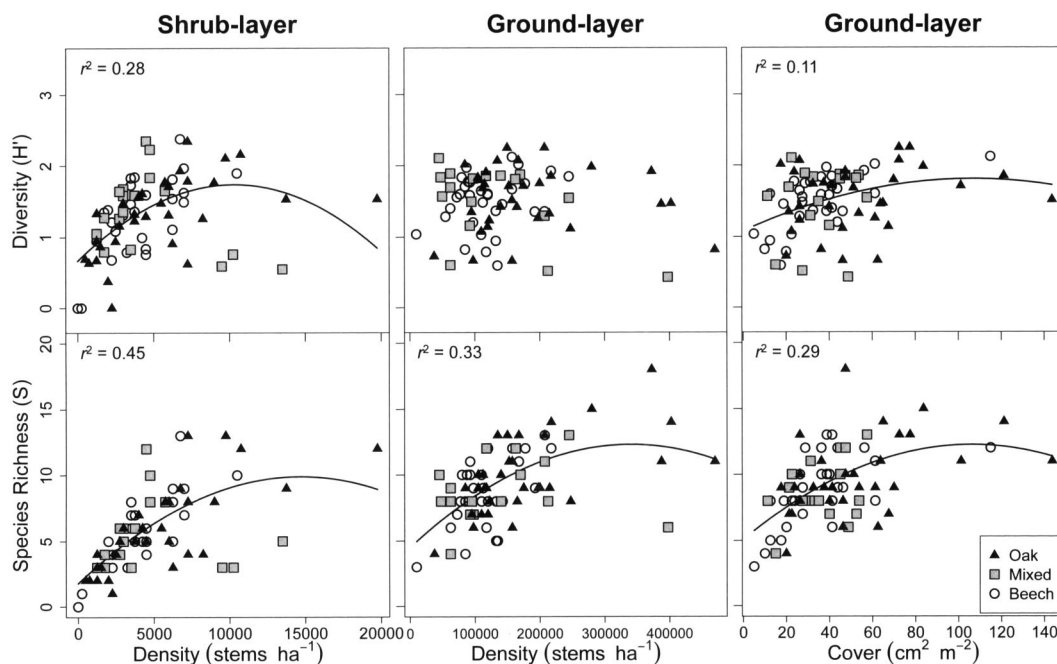
FIG. 3. Quadratic regressions between measures of diversity and surrogate measures of productivity for shrub- and ground-layer plots ($n = 80$) sampled in 2010. Measures of diversity are Shannon-Wiener diversity (H') and species richness (S). Surrogate measures of productivity are density (stems ha$^{-1}$) for the shrub-layer and density (stems ha$^{-1}$) and cover (cm$^2$ m$^{-2}$) for the ground-layer. Adjusted $r^2$ values are given for statistically significant regressions ($P < 0.01$).

were minor, except for a few significant increases in ground-layer density/cover (*Q. alba*, *Q. montana*, and *Q. velutina*).

The results of this study suggest that our Appalachian old-growth forest may not be experiencing the oak-to-maple dominance shift in the same way as second-growth forests. The tree regeneration layer in second-growth forests is usually dense with shade-tolerant species, which are believed to suppress oaks via competitive interactions (Arthur et al. 1998, Albrecht and McCarthy 2006). In old-growth systems, such competitive interactions may be moderated by relatively lower stem densities (Muller 1982, Fralish et al. 1991, Tyrrell and Crow 1994, Tappeiner et al. 1997), allowing *Quercus* populations to persist. The increase in *Acer* seedlings in BEH is consistent with other studies of oak-maple dynamics (Lorimer 1984, Parker et al. 1985, Host et al. 1987, Pallardy et al. 1988, Shotola et al. 1992, Abrams 1998), but the decrease in *Acer* sapling abundance was unexpected and likely a combined result of the fire disturbance and recruitment to the midstory over the past ten years. McEwan and Muller (2006) described a

pattern wherein *Quercus* species regeneration was restricted to the most xeric areas of the BEH watershed where mesophytic species should have less of a competitive advantage. The stability of *Quercus* shrub- and ground-layer populations over the past ten years may be a reflection of persistence within a range that has constricted to include these favorable habitats.

Compositional shifts, such as the "mesophication" of eastern North American forests (Nowacki and Abrams 2008), have the potential to alter environmental resource gradients as well as species diversity. These changes may, in turn, influence productivity, which is believed to exhibit a unimodal relationship with diversity (Al-Mufti et al. 1977, Grime 1979, Huston 1979, Grace 1999). Using density and cover as surrogate measures of productivity, our results showed that at a local scale, diversity-density and diversity-cover relationships exist in the shrub- and ground-layers of an old-growth Appalachian forest. We also found that these relationships were better described by quadratic, rather than linear, relationships. The density and cover
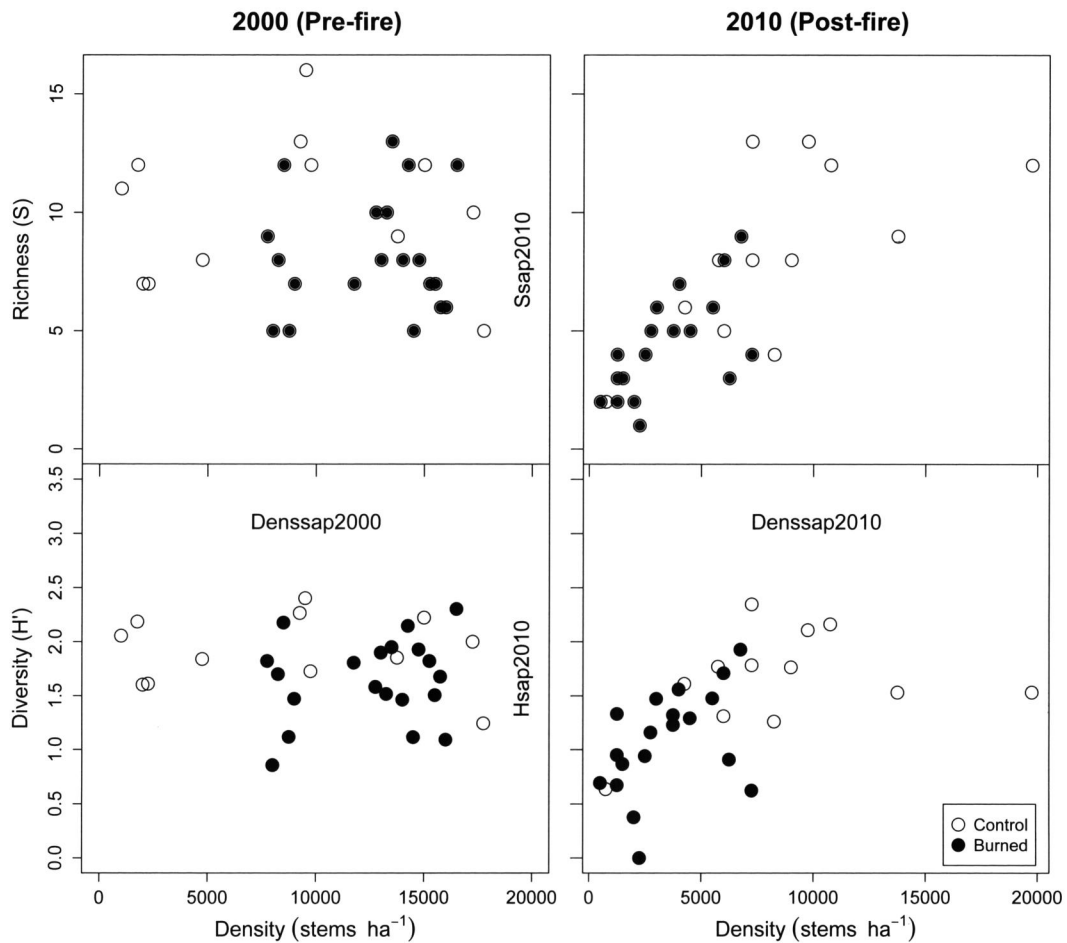
FIG. 4. Shrub-layer diversity-density and richness-density relationships within the Chestnut oak community plots ($n = 32$) in 2000 (pre-fire) and 2010 (post-fire). Solid circles indicate plots impacted by wildfire in May 2010 ($n = 20$), and open circles represent control plots (not burned, $n = 12$).

gradients created at this local scale are likely driven by the range of environmental conditions captured by the variety of plot elevations (375–553 m), aspect positions, (north-, east-, and south-facing) and slope percentages (27–90%) across the watershed (McEwan et al. 2005a). Productivity gradients are also likely influenced by a heterogeneous understory light environment resulting from canopy gap dynamics (Runkle 1982).

Prescribed fire is one proposed method for promoting oak regeneration in the eastern deciduous forests of North America (Van Lear and Watt 1993, Watt et al. 1993), but results vary depending on fire frequency, intensity, and seasonality (Arthur et al. 1998, Hutchinson et al. 2005, Albrecht and McCarthy 2006). The 2010 fire in BEH had impacts on the woody understory similar to those seen in

other single-fire studies, with an initial reduction in shrub-layer density and increased ground-layer density (Arthur et al. 1998, Hutchinson et al. 2005, Albrecht and McCarthy 2006, Elliot and Vose 2010). Ground-layer diversity and richness were unaffected, while shrub-layer richness was reduced such that, for the overall oak community, a linear and positive relationship between density and richness was created. It is unknown whether this relationship, as well as the fire-induced compositional changes in the ground- and shrub-layer communities, will impact long-term dynamics or be an ephemeral response that disappears with time (Hutchinson et al. 2005, Glasgow and Matlack 2007, Elliot and Vose 2010).

Fire may have also created the opportunity for colonization of new, undesirable, species in

the watershed (Huebner 2006, Kuppinger et al. 2010), which was previously free from invasive species (McEwan et al. 2005b). Three invasive plant species, *Ailanthus altissima*, *Paulownia tomentosa*, and *Rosa multiflora*, were found in the burned area of the watershed in 2010. First-year seedlings (mainly *A. altissima*) were present, as well as some larger individuals that had established in the years between samplings but prior to the fire. Monitoring these "nascent foci" (Moody and Mack 1988) is critically important to maintain the integrity of this unique forest ecosystem—we recommend management practices be employed to remove these invasive species.

**Conclusions.** The woody understory of oak forests across eastern North America are frequently sites of increasing dominance by mesophytic species (Nowacki and Abrams 2008, McEwan et al. 2011)—a pattern which is evident in the old-growth forest in BEH (McEwan et al. 2005a). *Acer rubrum* and *A. saccharum* were among the most important understory species, despite decreased *Acer* shrub-layer density, and equivocal changes in ground-layer *Acer* density and cover. In contrast, we found no evidence for significant losses of *Quercus* in the shrub- and ground-layers, which lends support to the McEwan and Muller (2006) suggestion that "the most xerophytic sites in the watershed may serve as refugia for oaks." While a strong oak-to-maple shift was not strongly evident, our study only covered a ten-year sampling interval, which may not be long enough to see trends of a successional trajectory known to operate over a much longer time-scale (Nowacki and Abrams 2008). In addition, our old-growth site is not subject to the anthropogenic influences that help drive oak-to-maple succession in second-growth forests (Nowacki and Abrams 2008, McEwan and Muller 2011), thus compositional shifts in BEH may be occurring at a slower rate relative to more disturbed forests.

We found evidence for unimodal relationships between diversity and surrogate measures of competition/productivity (density and cover) in the shrub- and ground-layer. Although the general relevance of a unimodal relationship between diversity and productivity has been a subject of interest in ecology (Oksanen 1996, Rapson et al. 1997, Liira and Zobel 2000, Chase and Leibold 2002), the

occurrence of this relationship in forest understories is relatively unexplored. Further work is needed to disentangle the environmental factors (e.g., moisture, light, and soil nutrients) that may influence stem density, cover, and diversity of the woody understory, and longer-term studies could reveal how these diversity-density and diversity-cover relationships are being influenced by compositional shifts in eastern deciduous forests of North America.

In the oak community, which was partially influenced by a 2010 wildfire, we found that shrub-layer density and richness decreased. A surprising outcome of this fire was the creation of an apparently linear relationship between density and richness in the woody understory of the oak community caused by changes in the burned plots. This may be a simple, *de facto* (or mathematical) outcome with fire-related loss of density and richness; however, the implications of this change for the oak community are ecologically interesting. The fire may also have promoted the establishment of invasive species in the watershed. This, coupled with the recent arrival of hemlock woolly adelgid has the potential to massively alter stand dynamics of BEH. The existing baseline data creates a unique opportunity to monitor the reaction of this old-growth forest to multiple, interacting, perturbations.

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