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Ten years of forest change in two adjacent communities on the southern Cumberland Plateau, U.S.A.

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REID, J. L., J. P. EVANS (Landscape Analysis Lab, Department of Biology, University of the South, Sewanee, TN 37383), J. K. HIERS (Joseph W. Jones Ecological Research Center at Ichauway, Rt. 2 Box 2324, Newton, GA 39870), AND J. B. C. HARRIS (Landscape Analysis Lab, Department of Biology, University of the South, Sewanee, TN 37383). Ten years of forest change in two adjacent communities on the southern Cumberland Plateau, U.S.A. J. Torrey Bot. Soc. 135: 224–235. 2008.—Forests of the Cumberland Plateau physiographic province have undergone significant change over the past century due to anthropogenic disturbances, and the magnitude and direction of this change will have important consequences for forest management and biodiversity conservation. Cove and upland forest communities on the Cumberland Plateau are in close proximity to one another, but have maintained distinct composition due to soil differences. Several anthropogenic influences common to other southern Appalachian forest communities, including fire suppression, predator removal, and introduction of pathogens, continue to drive change in these forests but remain relatively undocumented. In this 10-year study of these two major forest types, those disturbances were expected to homogenize cove and upland forests, with compositions increasingly dominated by generalist species, similar to trends elsewhere. Composition and structure were considerably altered in both communities over the course of this study, but non-metric multidimensional scaling showed that the cove and uplands remained distinct. Both communities were experiencing a steady replacement of *Quercus* species by *Acer* species, but *A. saccharum* and *A. rubrum* dominance were limited to the cove and uplands respectively. *A. saccharum* expansion in the coves is in contrast to trends reported in other studies of Appalachian forests. Replacement of *Quercus* species by *Acer* species was more advanced in the high-productivity cove forest; however, the trajectory of change was more consistent among upland forest plots. Documenting long-term status and trends in these forested communities will be critical for managing disturbance regimes and predicting consequences for regional biodiversity.

Key words: forest change, mixed mesophytic forest, oak regeneration, old-growth forests, Cumberland Plateau.

The mixed hardwood forests of the Cumberland Plateau extend in range over 63,840 km^2 from West Virginia, Virginia, and Kentucky south through Tennessee to northern Alabama (Austin 1981). These are among the highest conservation-value forests remaining in North America (Evans 2005). Like many of the forested communities in the southern Appalachians over the past century, these forests have been exposed to a suite of anthropogenic disturbances, which have dominated the dynamics of community development (Hinkle et al. 1993, Hiers and Evans 1997, Arthur et al. 1998). Unlike other physiographic provinces in the Southern Appalachian region, these forests are not well represented in the forest literature with few studies documenting long-term change across major forested communities.

In southern Tennessee, the Cumberland Plateau contains two major forest types, an upland forest and a cove forest (Hinkle 1993). Though similar in composition to the remainder of the Southern Appalachians, these forests differ in that tree assemblages are distinct and well-defined with few ecotones resulting from slope, precipitation, or elevational gradients (Braun 1950). Rather, cove and upland forests are distinguished by stark differences in underlying soil types (Hinkle 1993, Evans et al. 2002). Previous studies have described the xeric upland forest as composed predominantly of *Quercus* species in the canopy with *Acer rubrum* L., *Oxydendrum arboreum* (L.) DC, and *Nyssa sylvatica* Marsh.

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common in the understory (Thor et al. 1969, Ramseur and Kelly 1981). This is the dominant cover across the gently rolling topography of the plateau's sandstone cap (e.g., Hinkle 1989). The adjacent cove forest has a diverse, mixed mesophytic canopy with a *Quercus* component and *Acer saccharum* Marsh. dominated understory and midstory (McGee 1986, Hinkle 1989). Some studies have addressed the compositional differences between the upland and cove communities (Hinkle 1989), but little research has been done on structural differences or on the dynamics of forest change over longer periods of time (Hiers and Evans 1997).

Due to the close proximity of the upland and cove forests, it was once thought that the two communities were successional gradations of one "climatic climax" community (Braun 1950). Such deterministic theory has been replaced by a greater understanding of disturbance-based forest dynamics in the eastern deciduous forest (Bormann and Likens 1979, Sprugel 1991, Reice 1994). These disturbances represent any discrete event that disrupts function, composition, structure, physical environment, or resource availability (Pickett and White 1985). Canopy disturbances change light availability and in some cases (e.g., fire) alter soil composition and reduce litter accumulation (Hiers et al. 2007). Across much of the Southern Appalachians, small canopy gaps promote the establishment of tree species that do not regenerate competitively under a closed canopy (Phillips and Shure 1990). These gap-phase dynamics are thought to be central to the forest growth cycle and determination of floristic composition in the eastern deciduous forest (Whitmore 1989), however, gap-phase dynamics alone may not be sufficient for the maintenance of biodiversity on the Cumberland Plateau.

Contemporary natural disturbances on the Cumberland Plateau include ice storm damage, localized wind storm blow-downs, and southern pine bark beetle (*Dendroctonus frontalis*) outbreaks (Price et al. 1992, Evans et al. 2002). Pine bark beetle outbreaks reoccur on a 10–12 year cycle on the Cumberland Plateau and epidemics have been more spatially extensive in recent decades (Price et al. 1992). Historically, natural and anthropogenic fires also disturbed these communities (Hinkle et al. 1993), but the dynamic fire regimes on the Cumberland Plateau are only recently being addressed (Arthur et al. 1998). Plateau forests have also undergone many anthropogenic changes over the past century including the functional extinction of *Castanea dentata* Sudw. (Myers et al. 2004), the introduction of the dogwood blight (*Discula destructiva*) (Redlin 1991, Hiers and Evans 1997), fire suppression, acid rain (Kelly 1979, Kelly 1980), and increased browsing by white-tailed deer (*Odocoileus virginianus*) (Evans et al. 2002). At a landscape level, these forests have been further affected by fragmentation through ex-urban development and the widespread establishment of loblolly pine (*Pinus taeda* L.) for wood fiber production (Evans et al. 2002, Evans 2005).

Quercus presence in the Eastern Deciduous Forest has historically been maintained by periodic fires (Abrams 2003), and recent work on the Cumberland Plateau has demonstrated that repeated fires enhanced recruitment of several *Quercus* species (Arthur et al. 1998). Fire has been suppressed across much of the southern Cumberland Plateau for more than 60 years (Arthur et al. 1998). In the absence of fire, specialist *Quercus* species have steadily been replaced by generalist *Acer* species in many parts of the eastern deciduous forest (Abrams 1998, Abrams 2003) including the southern Appalachians (Elliott et al. 1999) and the southern Cumberland Plateau (McGee 1986, Arthur et al. 1998, Gilbert et al. 2003).

The purpose of this research was to initiate a long-term project to contrast the rate and direction of community-level change in the two major Cumberland Plateau forest types, which are each characterized by unique edaphic controls on species composition, despite their immediate adjacency. We specifically test the hypothesis that abundance of generalist species with little edaphic fidelity would increase across both communities (Elliot et al. 1999) in response to the suite of recent and parallel anthropogenic disturbances. If these disturbances cause convergence of forest structure and composition across such an extreme edaphic gradient, there may be significant long-term impacts on the biodiversity of the southern Cumberland Plateau.

Materials and Methods. We selected two study sites on the southwestern edge of the Cumberland Plateau in Franklin County, Tennessee, U.S.A. within and adjacent to Thumping Dick Hollow (Dick's Cove), a portion of an old-growth forest reserve owned by the University of the South. One site was located in the cove (545 m ASL), and the other was on the plateau uplands (570 m ASL). The plateau uplands are underlain by highly resistant Pennsylvanian-age sandstone, which weathers into thin, sandy, acidic soils that are water limited and have a low ion exchange capacity. Cove soils have a higher clay content derived from alternating layers of shale, sandstone, and limestone and consequently have greater soil moisture and ion exchange capacity (Francis and Loftus 1977, Mays et al. 1991). Both uplands and cove received the same annual precipitation (1.52 m; U.S. Dept. of Commerce 1976), however, they differed in moisture conditions due to variation in exposure, substrate, and canopy structure (Hiers and Evans 1997).

This forested area was chosen because it typifies land-use patterns on the southern Cumberland Plateau. The cove forest at our study site has not been selectively logged since at least 1900 and has never been clearcut due to its inaccessibility and protection by the University (Hinkle et al. 1993). The plateau upland forest is old second-growth, which is typical of mixed-oak forests on the southern Cumberland Plateau (Ramseur and Kelly 1981). Half of the upland plots were selectively harvested in 1976 using a 14-inch diameter-limit cut while the other half have not been logged for at least 50 years. The difference in land-use history between upland plots is manifested by a significantly lower basal area of trees > 20 cm diameter at breast height (DBH) in plots that were cut 30 years ago (*t*-test, $P = 0.002$ in 1995, $P = 0.045$ in 2005).

Sampling was conducted in September and October of 1995 and 2005. Sixteen paired plots were established within Dick's Cove and on the plateau surface. On the east and west sides of Dick's Cove we placed a 200 m transect in the cove and on the plateau upland surface. Plots were randomly selected along these four transects which parallel the bluff edge on either side. A nested sampling design was used at each plot location. Using 0.1 ha circle plots (radius 17.8 m), all canopy trees (DBH > 20 cm) were measured. Nested within this larger area was a 0.05 ha plot (radius 12.6 m) in which all midstory individuals (> 1.5 m in height) were measured for DBH and recorded in three size classes, 0–2.5 cm DBH, 2.5–10 cm DBH, and 10–20 cm DBH. Nested within this circle was a third plot 0.001 ha in size (radius 5.6 m) in which we recorded all understory individuals (< 1.5 m in height).

Similarity measures were used to determine how closely plots in 2005 resembled plots in 1995 based on density of species. We selected a proportional similarity index (i.e., percent similarity based on relative density) because of its flexible use in diverse communities (Provencher et al. 2002) and because it incorporates a relative measure of abundance (Brower et al. 1989). Proportional similarity (PS) for each of the 16 plots was calculated following the methods of Provencher et al. (2002). A $PS = 0$ indicates no similarity between the assemblages of two plots and a $PS = 1$ signifies perfect similarity of relative abundance of two assemblages.

We compared size-class distributions between cove and upland plots and between plots in 1995 and 2005 using chi-squared and Cochran-Mantel-Haenszel tests (MH; Mantel and Haenszel 1959, Agresti 1990, R Development Core Team 2005). The MH test looks for an association between variables in the table (location, year, size-class distribution), and it allowed us to account for differences between the east and west sides of the plateau study sites, which had different land-use histories.

Non-metric multidimensional scaling (NMS) was used to analyze the directional movement in plots between sampling periods from each community. We selected 32 variables (Appendix A), which represented understory, midstory, and canopy dynamics. True diversity, species richness, basal area (BA), density, and proportion of total BA or density for selected functional groups (USDA, NRCS 2006) were included in all analyses. Variables were selected to best represent structural and compositional characteristics of each vegetative layer. True diversity was used because it possesses a uniform set of mathematical properties that are more consistent with the concept of biological diversity—contrasted to entropies such as the Shannon-Weiner Index (Jost 2006). Midstory basal area was calculated using mean values of size class categories and stem densities. All ordinations included data from both forest types from 1995 and 2005. Data were analyzed in PC-ORD using Sorenson distance measures and random starting coordinates (McCune and Meffrod 1999). Monte Carlo tests of stress in relation to dimensionality were generated from 50 randomized runs of plot data. Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space were used to calculate variation explained in the final ordination (McCune and Meffrod 1999).

Results. FOREST COMPOSITION. Upland and cove communities were dominated by different species in all size-classes. The upland canopy (> 20 cm DBH) community was dominated by *Quercus coccinea* Muenchh., *Q. prinus* L., *Q. alba* L., and *Oxydendrum arboreum* in 1995 and 2005 (Table 1). Mortality in *Q. coccinea* and recruitment of canopy individuals in *Q. prinus* resulted in a rank order change of abundance for these two upland canopy species (Table 1). In the cove, *Nyssa sylvatica* and *Acer saccharum* increased in the canopy (+30% and +66% respectively), while abundance of *Carya ovata* (P. Mill.) K. Koch decreased (−8.3%). The annual canopy mortality rate was 0.67% of stems in upland plots and 0.84% of stems in the cove plots, but did not differ significantly between forest types (P = 0.598). Fifty percent of upland canopy mortality was attributed to loss of *Q. coccinea* and 40% of cove canopy mortality was attributed to the loss of *Q. rubra* L.

Midstory (< 25 cm DBH) composition was dominated in the upland community by *Vaccinium* species, *Nyssa sylvatica*, *Sassafras albidum* (Nutt.) Nees, and *Acer rubrum* in both 1995 and 2005 (Table 1). All upland species decreased in midstory density over the 10 years except *A. rubrum* (+54%). Cove midstory composition was dominated in both years by *A. saccharum*. All species in the cove decreased in midstory density over the 10 years except *Asimina triloba* (L.) Dunal (+450%).

Understory (< 1.5 m height) species composition was dominated by *Vaccinium* species and *Sassafras albidum* in the upland community and by *Acer saccharum*, *Liriodendron tulipifera* L., and *Fraxinus americana* L. in the cove (Table 1). *Quercus coccinea* increased by 77% in the understory in the upland community over the 10 years. There was little change in understory composition in the cove.

Cove and upland communities did not converge compositionally over the 10-year study period but showed parallel trends of forest change. There was little compositional overlap between upland and cove communities in 1995 (mean proportional similarity = 0.074 ± 0.011) and 2005 (mean proportional similarity = 0.056 ± 0.014). This change in similarity from 1995 to 2005 was not significant (t-test, $P = 0.371$). Much of the difference in stem densities between cove and upland communities resulted from an abundance of *Vaccinium* species and *Sassafras albidum* in the understory of the upland community, however, when *Vaccinium* species and *S. albidum* were removed from the analysis, mean proportional similarity between the communities was still low: 0.130 ± 0.013 in 1998 vs. 0.109 ± 0.033 in 2005. Compositional change (*Vaccinium* species and *S. albidum* included) was more rapid in the cove than the uplands as proportional similarity between cove plots in each year (0.604 ± 0.031) was significantly lower than between upland plots in each year (0.869 ± 0.010; t-test, $P < 0.001$).

FOREST STRUCTURE. Size-class distribution was not independent of location or time (X^2 = 2706.098, $P < 0.001$, d.f. = 13; Fig. 1). There was a significant difference in size-class distributions between upland and cove in 1995 (Mantel-Haenszel mean score test, $P < 0.001$) and in 2005 (Mantel-Haenszel mean score test, $P < 0.001$). In both years, this difference can be attributed to greater understory and canopy density on the uplands (Fig. 2). Understory density on the uplands was 9831 ± 1600 stems/0.1 ha in 1995 and 9283 ± 607 stems/0.1 ha in 2005; whereas the cove understory was depauperate in both years with 1001 ± 183 stems/0.1 ha in 1995 and 1170 ± 338 stems/0.1 ha in 2005. Mean canopy density was greater on the uplands than in the cove in 1995 (+7 ± 2 stems/0.1 ha) and in 2005 (+9 ± 2 stems/0.1 ha)

Differences in land-use history in the uplands on the east and west sides of the study area were reflected by changes in size-class distribution in this cover type. There was a significant difference between size-class distributions of upland plots in 1995 and in 2005 (Mantel-Haenszel mean score test, P = 0.007) that may be attributed to a decrease in midstory stems 0–2.5 cm DBH on the east side of the Dick's Cove uplands (−164 ± 39 stems/0.1 ha). On the west side of the study area, midstory trees 0–2.5 cm DBH increased by 37 ± 46 stems/plot. Losses among trees 0–2.5 cm DBH on the east side of the cove were primarily *Vaccinium* species (−59 ± 43

Table 1. Density in woody stems per 0.1 ha of upland and cove communities in Dick's Cove, 1995–2005. Bold numbers indicate ranks for each column. Species composing "Other": *Amelanchier arborea* (Michx. f.) Fern., *Viburnum acerfolium* L., *Celtis occidentalis* L., *Aesculus flava* Ait., *Juniperus virginiana* L., *Illex verticillata* (L.) Gray, *Magnolia acuminata* (L.) L., *Ulmus rubra* Muhl., *Morus rubra* L., *Illex opaca* Ait., *Azalea* spp., *Pinus strobus* L., *Diospyros virginiana* L., *Quercus muehlenbergii* Engelm., *Liquidambar styraciflua* L., *Vaccinium arboreum* Marsh., *Rhus copallinum* L., *Ulmus alata* Michx., *Viburnum rufidulum* Raf., *Castanea dentata* (Marsh.) Borkh., *Rhamnus* spp., and *Quercus stellata* Wangenh. Overstory was defined as all canopy trees > 20 cm DBH; midstory individuals were > 1.5 m in height and recorded in 3 size classes, 0–2.5 cm DBH, 2.5–10 cm DBH, and 10–20 cm DBH, understory included seedling and individuals < 1.5 m in height.

	Canopy				Midstory				Understory			
	Upland		Cove		Upland		Cove		Upland		Cove	
Species	1995	2005	1995	2005	1995	2005	1995	2005	1995	2005	1995	2005
Quercus coccinea	6.9 **1**	6.3 **2**	0.0	0.0	7.0	2.3	0.0	0.0	276.3	490.0 **5**	0.0	0.0
Quercus prinus	6.1 **2**	7.1 **1**	0.6	0.8	16.8	11.5	0.5	0.0	706.3 **4**	550.0 **4**	7.5	3.8
Quercus alba	4.3 **3**	4.8 **3**	2.3 **2**	2.5 **2**	30.8 **4**	18.8	1.8	0.8	326.3 **5**	317.5	48.8	22.5
Oxydendrum arboreum	1.3 **4**	1.4 **4**	0.1	0.1	28.5	25.3 **4**	1.3	0.5	21.3	37.5	2.5	0.0
Quercus velutina	1.0 **5**	1.0 **5**	0.3	0.3	4.0	1.0	0.0	0.0	143.8	131.3	0.0	0.0
Nyssa sylvatica	0.9	0.9	1.3	1.6 **5**	53.5 **2**	37.3 **3**	6.8	2.5 **5**	152.5	167.5	161.3 **4**	101.3 **4**
Carya tomentosa	0.8	0.8	0.0	0.0	20.3	12.3	0.0	0.0	98.8	73.8	7.5	0.0
Carya glabra	0.4	0.4	1.5 **4**	1.6 **4**	3.8	3.3	3.8	1.0	52.5	52.5	25.0	3.8
Acer rubrum	0.4	0.4	0.0	0.0	30.0 **5**	46.3 **2**	0.8	0.5	745.0 **3**	665.0 **3**	15.0	33.8
Robinia pseudoacacia	0.1	0.1	0.3	0.0	9.0	3.0	0.0	0.5	51.3	15.0	8.8	40.0
Sassafras albidum	0.1	0.4	0.0	0.0	45.0 **3**	19.8 **5**	0.8	0.8	3162.5 **2**	2998.8 **2**	18.8	1.3
Carya cordiformis	0.1	0.1	0.3	0.1	0.3	0.0	0.8	0.0	3.8	3.8	16.3	1.3
Acer saccharum	0.0	0.0	1.5 **5**	2.5 **3**	1.8	2.5	243.8 **1**	159.0 **1**	6.3	6.3	362.5 **1**	800.0 **1**
Fraxinus americana	0.0	0.0	0.3	0.3	0.3	0.0	7.3 **4**	0.3	1.3	1.3	212.5 **3**	266.3 **2**
Liriodendron tulipifera	0.0	0.0	1.3	1.3	0.0	0.0	7.3 **5**	4.3 **3**	11.3	3.8	281.3 **2**	125.0 **3**
Lindera benzoin	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.5	0.0	0.0	91.3 **5**	55.0 **5**
Cercis canadensis	0.0	0.0	0.0	0.0	0.0	0.0	14.0 **2**	4.8 **2**	0.0	0.0	40.0	23.8
Quercus rubra	0.0	0.0	3.1 **1**	2.6 **1**	0.0	0.0	0.0	0.0	0.0	0.0	3.8	22.5
Carya ovata	0.0	0.0	1.6 **3**	1.5	0.5	0.5	1.0	0.5	0.0	0.0	32.5	21.3
Prunus serotina	0.0	0.0	0.1	0.3	1.5	1.3	4.0	1.5	30.0	30.0	30.0	11.3
Vaccinium spp.	0.0	0.0	0.0	0.0	87.8 **1**	71.0 **1**	0.0	0.0	3870.0 **1**	3647.5 **1**	5.0	3.8
Cornus florida	0.0	0.0	0.0	0.0	9.3	3.0	13.0 **3**	1.0	6.3	1.3	7.5	0.0
Kalmia latifolia	0.0	0.0	0.0	0.0	10.8	6.3	0.0	0.0	87.5	17.5	0.0	0.0
Asimina triloba	0.0	0.0	0.0	0.0	0.0	0.0	0.5	2.8 **4**	0.0	0.0	0.0	0.0
Tilia americana var. *heterophylla*	0.0	0.0	0.3	0.3	0.0	0.0	3.0	2.5	0.0	0.0	0.0	0.0
Juglans nigra	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other	0.0	0.0	0.0	0.0	5.3	2.8	4.8	2.8	78.8	72.5	37.5	13.8
TOTAL	22.3	23.5	14.9	15.9	365.8	267.8	316.0	186.3	9831.3	9282.5	1415.0	1550.0

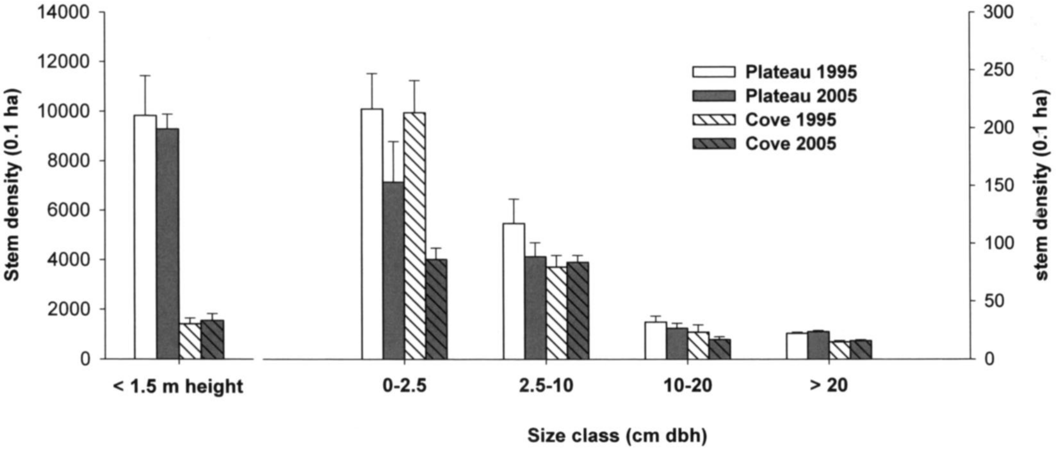

FIG. 1. Size class distributions of woody plant species in an upland and adjacent cove community in Dick's Cove (Sewanee, TN) from 1995–2005. Categories on the x-axis are size classes in diameter at breast height (DBH).

stems/0.1 ha), *Sassafras albidum* (−35 ± 18 stems/0.1 ha), and *Nyssa sylvatica* (−13 ± 3 stems/0.1 ha). Losses among trees 2.5–10 cm DBH on the east side of the cove were primarily *S. albidum* (−17 ± 10 stems/0.1 ha) and *Quercus alba* (−11 ± 5 stems/0.1 ha). In non-clonal species, a sustainable size-class distribution is defined as having a balance in

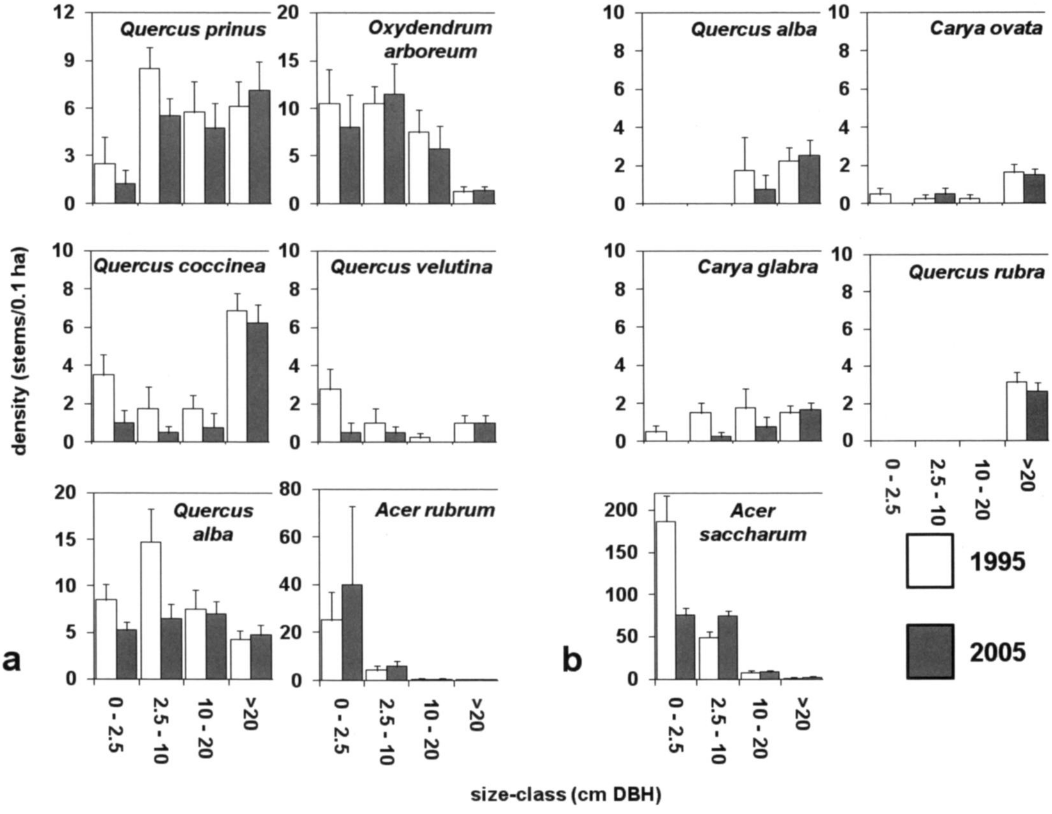

FIG. 2. Size-class distributions of dominant canopy (> 20 cm DBH) and midstory (0–20 cm DBH) tree species in an upland (a) and adjacent cove community (b) in Dick's Cove from 1995–2005. Categories on the x-axis are size-classes (cm DBH). Values on the y-axis are density (stems/0.1 ha).

recruitment and mortality, indicated by an inverse-J curve (Schmalzer 1988).

There was also a significant difference between size-class distributions of cove plots in 1995 and in 2005 (Mantel-Haenszel mean score test, $P = 0.03$). This difference can be attributed to a dramatic decrease in trees 0–2.5 cm DBH over the 10 year period (-127 ± 28 stems/0.1 ha). Decreases in *Acer saccharum* (-111 ± 29 stems/0.1 ha) were at least an order of magnitude greater than decreases in any other species in that size-class. Only *A. saccharum* had a stable size-class distribution.

NON-METRIC MULTIDIMENSIONAL SCALING. A 2-dimensional solution was recommended and represented the most parsimonious fit (Fig. 3a) The stress for the final NMS 2-dimensional ordination was 6.5217, with a Monte Carlo test showing statistical significance ($P = 0.020$). Axis 1 had an R^2 value of 0.071 and Axis 2 had an R^2 of 0.747. The cumulative R^2 for the 2-dimensional ordination was 0.818 or nearly 82% of variation in plots space explained by the final 2-dimensional ordination.

Axis 1 represents the gradient of midstory stem density and basal area while axis 2 is defined by increasing overstory basal area and increasing midstory stems of species that are both wind-dispersed and shade-tolerant (Fig. 3a). Variation in axis 2 also shows a gradient of decreasing seedling density and decreasing resprouts in the understory. When arrows are used to map the direction of movement in each plot from 1995–2005, upland plots show a strong directional decrease in midstory BA (Figure 3b), with some plots increasing in wind-dispersed species and canopy BA.

Cove plots were defined on axis 2 by a closed canopy forest dominated by midstory shade-tolerant and wind-dispersed species (primarily *Acer saccharum*). Upland plots were defined on axis 2 by greater understory density, particularly amongst species with the potential for root-sprouting. Greater understory density and less shade-tolerant species in the midstory of the upland community may be attributed to its more open canopy structure. Midstory basal area defined variation in both cove and upland plots along axis 1.

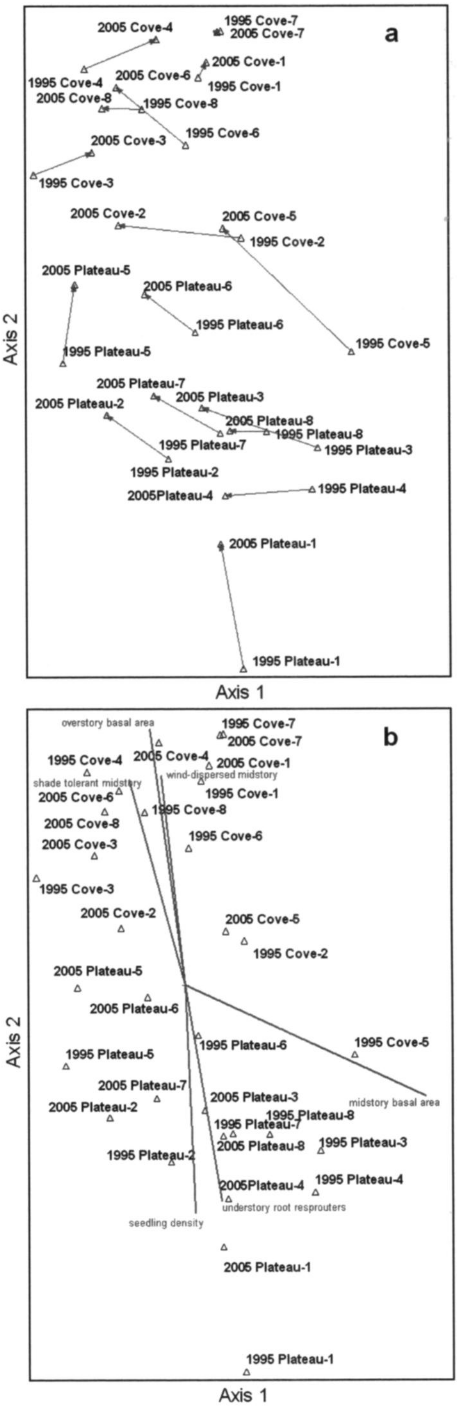

FIG. 3. Non-metric multidimensional (NMS) scaling ordination of two adjacent forest communities in Dick's Cove. (a) NMS bi-plot showing vectors. (b) NMS with vectors showing plot movement over time.

The movement of upland plots was directional. Plots moved towards greater canopy basal area and less midstory basal area. Cove plots do not respond as a group over this time period, instead they show more diverse patterns of direction and magnitude of change. Some plots (Cove-2, Cove-6, and Cove-7) moved towards less midstory basal area, while others (Cove-3, Cove-4) moved towards greater midstory basal area. Cove and upland plots were clustered and remained separate from one another over the 10-year study.

Discussion. Over much of the southern Appalachians, forest communities vary gradually with elevation and across environmental gradients (Whittaker 1956, Day and Monk 1974, Elliott et al. 1999). The Cumberland Plateau differs from forests in those studies since soil types rather than elevation are the primary factors maintaining the distinctness of juxtaposed upland and cove communities (Hinkle et al. 1993, Arnold et al. 1996, Evans et al. 2002). Mesic and xeric sites in this study represent extreme ends of previously studied ecological gradients in this region. Due to these extreme differences, cove and upland forest communities maintained species-level distinctness while being in close proximity to one another and possessing few barriers to seed dispersal. We did not find the hypothesized convergence of cove and upland flora through colonization by shared generalist species, instead we found convergence occurring at the genus level and at the level of functional guilds. This convergence was characterized by increased *Acer* populations, *Quercus* decline, increased wind-dispersed midstory, and increased shade-tolerant midstory.

While both communities experienced an increase in *Acer* abundance, *A. rubrum* and *A. saccharum* were restricted with little overlap to the upland and cove habitats respectively, likely resulting from differences in soil moisture and edaphic conditions (Abrams 1998). Increased relative abundance of generalist *A. rubrum* in the plateau forest is consistent with the large volume of literature on the eastern deciduous forest (Lorimer 1994, Abrams 1998, Pierce et al. 2006). *Acer* dominance in the cove forest was more advanced than in the upland forest. This trend may be the result of time since the most recent fire event. Fire has been absent from the study area for > 60 years, however, the long-term fire history of this study area is unknown. Advanced *Acer* dominance in the cove could also be explained by greater site productivity in that habitat. As site quality improves, photosynthesis increases, and vegetation experiences more rapid turnover of leaves, fine roots, and other tissues (Hendricks et al. 1993). It follows that tree turnover and compositional change would be greater in the cove than on the uplands. The expectation of more rapid turnover in the cove was borne out by proportional similarity analyses, where cove plots experienced much greater compositional change than corresponding upland plots.

In a central Indiana hardwood forest characterized by limestone-derived soils, Spetich and Parker (1998) showed that the midstory composition of an old-growth forest had changed from 14% *Quercus* species and 12% *Acer saccharum* in 1926 to 1% *Quercus* and 43% *A. saccharum* by 1992. On the Allegheny Plateau in Pennsylvania, however, there has been a decline in *A. saccharum* density on sites with acidic soils where tree growth is limited by base cation deficiencies (Drohan 2000, Drohan et al. 2002). It is likely that this decline was exacerbated by high levels of acid precipitation within the region (Sharpe 2002). Acid precipitation on the Cumberland Plateau likely serves to restrict the distribution of *A. saccharum* to the limestone-derived soils of the coves by inhibiting its spread onto the acidic soils of the plateau surface.

Coincident with increases in *Acer* species on the Cumberland Plateau is the decline of *Quercus* species in both upland (Arthur et al. 1998, Myers et al. 2004) and cove habitats (Galbraith and Martin 2005). Both fire suppression and increased deer browse have been suggested as potential limitations on *Quercus* regeneration (Arthur et al. 1998, Abrams 2003). We found a high incidence of *Quercus* mortality in the canopy and declining *Quercus* densities in the midstory of both the cove and upland communities. The pattern of oak decline being more pronounced within the red oak group (*Q. rubra*, *Q. coccinea*, and *Q. velutina* Lam.) than among white oaks (*Q. prinus* and *Q. alba*) is consistent with other mortality studies from many different Southern Appalachian forest stands (Starkey et al. 1989, Stringer et al. 1989). The *Q. rubra* population in Dick Cove continues to exhibit evidence of canopy mortality and regeneration failure first identified by McGee (1986). *Q.*

rubra regeneration has been shown to be severely limited by interspecific competition at the sapling stage from species such as *Acer* species (Lorimer et al. 1994) and by deer browse (Buckley et al. 1998). High levels of canopy mortality in *Q. coccinea* and *Q. velutina* in upland habitats have been attributed to drought and the interaction of drought with diseases such as *Armillarria* (Stringer et al. 1989). The southern Cumberland Plateau experienced a period of major summer drought within the time period of this study (1999–2001). In constrast to *Q. coccinea*, *Q. prinus* had a relatively stable size class distribution and actually replaced *Q. coccinea* as the most abundant upland canopy species (Table 1). *Q. prinus* is generally considered highly drought-tolerant (Mikan et al. 1994) and has been identified as being more of a habitat generalist in southern Appalachian forests as compared to other oak species (Elliott et al. 1999). Although *Quercus* species are not in danger of being extirpated from these communities, an overall reduction in canopy abundance could decrease tree diversity and have negative impacts on animals that rely on hard mast for food (Christisen and Korshgen 1955, Wolff 1996, Rodewald 2003).

The dogwood blight epidemic, which spread into the Cumberland Plateau region by the late 1980s, resulted in a major loss of *Cornus florida* L. in both the upland and cove habitats (Hiers and Evans 1997). It is interesting to note that, while *C. florida* continued to decline in density between 1995 and 2005, we found surviving trees in both habitats that appear to be blight resistant. The loss of this once dominant understory species has been associated with a decline in available calcium in acidic forest soils such as those present in the upland Plateau habitat (Hiers and Evans 1997, Jenkins et al. 2007, Holzmueller et al. 2007) and with a loss of fall forage for migratory songbirds (Hiers and Evans 1997). Hiers and Evans (1997) found an increase in *Nyssa sylvatica* and *Lindera benzoin* (L.) Blume stem density in the cove understory following the loss of *C. florida*. However, both of these species showed a subsequent decline between 1995 and 2005 in both the midstory and understory size classes (Table 1). Observational evidence suggested that this was due to heavy deer browse on these species within the cove.

In addition to species composition, the directionality and magnitude of change in upland versus cove communities in this study may be explained through the interaction of anthropogenic disturbance with light availability and soil productivity. Upland forest dynamics are driven primarily by limited soil resource availability (Hinkle 1989). This is in contrast to cove forest dynamics, which are controlled by limited light availability (Martin 1992). Canopy mortality in the cove was not significantly greater than on the uplands, yet changes associated with gap-phase regeneration and growth (i.e., decrease in midstory basal area) were more dramatic in the cove community. Natural gap formation in both communities is dominated by windthrow; however, this disturbance alone may not have the same effects in the upland forest because it fails to change soil resource availability. Thus, community level response may be less dramatic—and of a different direction—on the uplands than in the cove forest where shade-intolerant species quickly colonize gaps.

In addition to windthrow, other disturbances or interruptions to the disturbance regimes may play a role in driving patterns of forest change. Arthur et al. (1998) suggest that fire enhances *Quercus* regeneration by eliminating competition with generalist species and opening microsites. Hiers et al. (2007) also found that litter accumulation is the primary factor limiting regeneration in xeric *Pinus palustris* Mill. ecosystems. A deep litter layer and O-horizon caused by low decomposition rates of xeric sites coupled with fire suppression could be the primary limitation on *Quercus* regeneration on the southern Cumberland Plateau. Litter accumulation may also favor clonal species that can invest more resources in pushing up sprouts (Hiers et al. 2007). A high abundance of such clonal (root-sprouting) species in the understory is one factor that characterizes upland forests in Dick's Cove.

Stochastic disturbances, both natural and anthropogenic, may change ecosystems in unpredictable ways (Reice 1994, Drury and Runkle 2006). Such non-equilibrium dynamics raise important challenges for community-scale research and conservation management, highlighting the need to document the trajectory and rate of change in forested ecosystems over longer periods of time. Moreover, understanding mechanistically the community response to particular managed disturbances, such as deer herbivory and fire, across a range of site conditions is now critical to conservation of regional biodiversity. The long-term application of periodic fires and intense deer-herd management may prove to be vital tools in sustaining *Quercus* forests (Horsley et al. 2003, Hutchinson et al. 2005) generally throughout the southern Appalachians and on the Cumberland Plateau specifically (Arthur et al. 1998). However, the details of such managed disturbances regimes, particularly fire, remain a matter of debate (Gilbert et al. 2003). Disturbances are central to the maintenance of biodiversity in the eastern deciduous forest, however, these events occur at a time scale that necessitates long-term monitoring and improved predictive models of community responses over the extensive Cumberland Plateau physiographic region.

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Canopy Variables	Midstory Variables	Understory Variables
pBA of rapid-growing species	pBA of rapid-growing species	pD of rapid-growing species
pBA of tolerant to highly tolerant shade-tolerant species	pBA of tolerant to highly tolerant shade-tolerant species	pD of intermediate to rapid-growing species
pBA of intermediate to highly tolerant shade-tolerant species	pBA of intermediate to highly tolerant shade-tolerant species	pD of tolerant to highly tolerant shade-tolerant species
pBA of wind-dispersed species	pBA of wind-dispersed species	pD of intermediate to highly tolerant shade-tolerant species
pBA of mammal-dispersed species	pBA of mammal-dispersed species	pD of mammal-dispersed species
pBA of basal-sprouting species	pBA of bird-dispersed species	pD of bird-dispersed species
Total BA	pBA of species with pH tolerance <4.6	pD of wind-dispersed species
Stem density	pBA of basal-sprouting species	pD of root-sprouting species
	pBA of root-sprouting species	Stem density
	Total BA	Species richness
	Species richness	True diversity
True diversity	True diversity	