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Decadal Changes in Disjunct Eastern Hemlock Stands at Its Southern Range Boundary

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ABSTRACT Species distribution modelling has revealed shifts in the spatial distribution of the range of eastern hemlock (*Tsuga canadensis* (L.) Carrière) in eastern North America. Models project a decline in eastern hemlock at the southern portion of its range, but not contraction of the southern boundary. In 2003, the vertical, horizontal, and diameter structure and diameter-age relationships of eastern hemlock were quantified in 10 stands thought to represent the species' 10 southernmost stands on the Cumberland Plateau in Alabama. In 2013, we resurveyed these stands to document changes in stand characteristics over the past decade. In addition, we explored additional reaches of stream corridors known to support eastern hemlock to document additional stands previously undescribed in the literature. Results from our resampling revealed that stands had similar stem frequencies over the 10-yr period, but, generally, the number of canopy stems and the number of seedlings declined. The decline in seedlings may have been a result of mortality or recruitment to larger size classes. The decline in canopy trees may have been caused by regional drought in 2007 or localized severe weather events. Our additional sampling yielded one stand not previously described. Although we cannot rule out additional disjunct stands in the area, we speculate that no eastern hemlock stands occur farther south than those documented here. Based on our results, we suggest that these stands are reproductively viable with episodic regeneration, and there has been no evidence of range contraction at the southern range limit over the past decade.
Key words: Alabama, disjunct, eastern hemlock (*Tsuga canadensis*), range migration, regeneration.

INTRODUCTION The potential range response to projected climate change, based on suitable habitat, has been modeled and mapped for many tree species in eastern North America (Iverson et al. 2008, Matthews et al. 2011). Species distribution models project the hypothesized spatial distribution of suitable environments for tree species in response to conditions that are expected to occur under different climate change scenarios (Guisan and Thuiller 2005, Prasad et al. 2007, Elith and Leathwick 2009). Model projections reveal a shift in the spatial distribution of suitable habitat for eastern hemlock (*Tsuga canadensis* (L.) Carrière) in accord with changing climatic conditions; however, the models project the species' southern boundary to remain relatively stable geographically (i.e., the species is expected to remain in northern Alabama, but at a lower abundance and/or dominance than at present [Iverson et al. 2008]).

During the late Pleistocene, forests of the southeastern USA were composed of many tree species that are now restricted to higher latitudes or that typically now only dominate stands at higher latitudes (Davis 1981, Delcourt et al. 1983). Davis (1981) hypothesized that the refugium for eastern hemlock during the late Wisconsinan glaciation was in the Appalachian Mountains, the Atlantic Coastal Plain, or on the then exposed continental shelf because of the lower sea level. More recently, Potter et al. (2012) analyzed range-wide genetic variation in eastern hemlock and suggested that three or four glacial refugia occurred in the southeastern USA. During the late Pleistocene and early Holocene, eastern hemlock likely spread from its refuge(s) and, by 16,000–20,000 yr before present (BP), was abundant throughout the southern Appalachian Highlands and adjacent provinces in the

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Mid-South region (Watts 1970, Delcourt et al. 1980). Segars et al. (1951) hypothesized that eastern hemlock did not likely occur on the Gulf Coastal Plain during this period, so that the southern range boundary coincided with the southern terminus of the Appalachian Highlands. Climatic warming during the early Holocene resulted in contraction of the southern range boundary for many tree species (Oosting and Hess 1956), with taxa such as eastern hemlock becoming restricted to sites with favorable microenvironmental conditions (Delcourt et al. 1983). Disjunct stands of eastern hemlock in Alabama, which represent the species' southern extent, likely represent remnants of the once more widespread distribution of the species during the late Pleistocene and early Holocene (Hart and Shankman 2005).

Eastern hemlock is a common component in Appalachian forests of eastern North America and, prior to the introduction and spread of hemlock woolly adelgid (*Adelges tsugae* Annand), often dominated riparian sites through the region. Eastern hemlock exhibits life-history characteristics that make it unique among many of the species with which it co-occurs. For example, it is a gymnosperm that generally only co-occurs with angiosperm species. It has a low light compensation point and can tolerate dense shade. Eastern hemlock often occurs in almost pure stands, especially on lower slopes and in riparian zones of Appalachian forests (Kessell 1979, Godman and Lancaster 1990, Ellison et al. 2005, Shankman and Hart 2007). The species is also among the longest-lived trees in the region, as individuals have been documented at more than 500 yr of age (Eastern OLDLIST 2014). Eastern hemlock is capable of sustaining slow growth for long periods in light-limited environments, but retains the ability to adjust quickly to additional growing space if it is made available via canopy disturbance (Kelty 1986, Foster and Zebryk 1993, Davis et al. 1996, Black and Abrams 2004). Eastern hemlock is considered a foundation species, as it controls population and community dynamics and regulates ecosystem processes (Orwig et al. 2002, Ellison et al. 2005). For example, eastern hemlock litter decomposes slowly, which often results in deep, acidic humus with low rates of nitrogen mineralization and nitrification (Rogers 1978, Finzi et al. 1998, Lovett et al. 2004). Stems of eastern hemlock often have dense and deep canopies and, as an evergreen, eastern hemlock trees transpire throughout the year. Thus, eastern hemlock trees may reduce the quantity and quality of light, reduce temperature, and modify humidity in understory environments (Hadley 2000, Catovsky et al. 2002, Rankin and Tramer 2002, Ellison et al. 2005, Ford and Vose 2006).

The native range of eastern hemlock extends from southern Quebec and Ontario southward along the Appalachian Highlands to Georgia and Alabama. Although the species is rather widely distributed, stand characteristics differ throughout its range (Ellison et al. 2005). Disjunct stands are common in the southern and western portions of its range, and stand characteristics and abiotic conditions of some isolated stands have been studied (Harper 1943, Friesner and Potzger 1944, Segars et al. 1951, Oosting and Hess 1956, Bormann and Platt 1958).

In 2003, Hart and Shankman (2005) sampled all eastern hemlock stands ($n = 10$) known to exist at the southern range limit of the species on the Cumberland Plateau in Alabama. They described the vertical and diameter structure of all eastern hemlock stems in each of the 10 known stands and also reported on the general characteristics of the stands, such as co-occurring canopy species and slope grade. The objectives of our study were to resurvey the stands inventoried in 2003 to document changes in stand characteristics over the past decade and to expand the search (i.e., explore additional reaches of streams on which eastern hemlock is known to occur) for additional eastern hemlock stands that were not described by Hart and Shankman (2005). Our results provide information on the viability of eastern hemlock stands at the southern range limit of the species, which may be used to test projections of eastern hemlock range migration in response to changing climatic conditions. In addition, as the hemlock woolly adelgid advances through the contiguous range of eastern hemlock, these outlying stands may represent the last of the species (Hart 2008) and quantifying their viability may aid in preservation efforts.

MATERIALS AND METHODS

Study Area

Our study took place near the southern terminus of the Cumberland Plateau in Alabama and extended through Fayette, Walker, and Jefferson counties (Figure 1). The southern range extent of eastern hemlock roughly

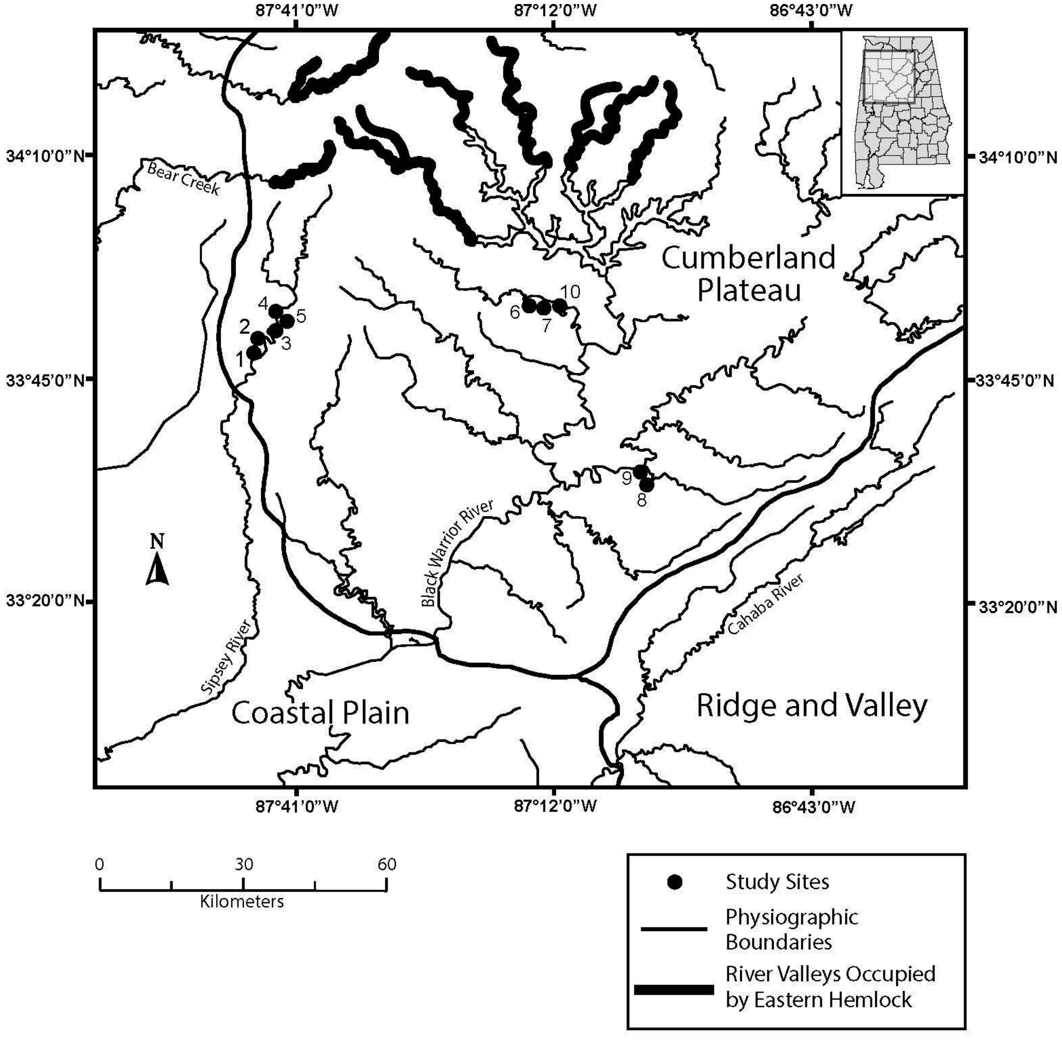

Figure 1. Map of study area on the Cumberland Plateau, Alabama. Note that stand 8 represents combined stands 8 and 10 from the 2003 survey and stand 10 represents the new stand found in the 2013 resurvey.

corresponds to the southern limit of the Cumberland Plateau (Shankman and Hart 2007). The Fall Line separates the Appalachian Highlands, including the Cumberland Plateau, from the Coastal Plain (Fenneman 1938). In Alabama, eastern hemlock occurs just north of the Fall Line, but does not exist naturally south of this physiographic belt. Each eastern hemlock stand sampled in this study occurred along permanent streams, and the stands typically did not extend more than 20 m away from the stream margins. The stands varied in length, but were all oriented parallel to the streams. With one exception (stand 9), all sampled stands occurred on steep slopes, and elevation ranged from 110 to 125 m above mean sea level (Hart and Shankman 2005). Each eastern hemlock stand occurred on shallow soils overlying sandstone of the Hartselle formation. Much of the sandstone along the river bluffs was exposed and covered with lichens and bryophytes. Cracks in the sandstone often supported vegetation, including eastern hemlock stems across a wide range of size classes. Even during the driest month of the year, October, water was typically available through surface seepage of the permeable sandstone layers that overlie impermeable rock strata (Lacefield 2000).

Field Data Collection and Analysis

All eastern hemlock stands known to exist at the southern boundary of the species were sampled in 2003 by Hart and Shankman (2005). They inventoried five stands in Fayette County, Alabama along the Sipsey River, two stands in Walker County along Blackwater Creek, and three stands in Jefferson County along Village Creek. We visited each of these stands during 2013. We also explored, via foot and canoe, other reaches of these streams to search for additional eastern hemlock stands not recorded previously. Our search was based on proximity to known eastern hemlock stands and topographic characteristics, and was largely concentrated on downstream reaches and tributaries to the south of known eastern hemlock locations. In each documented stand, we did a complete census of all eastern hemlock stems. Each eastern hemlock stem was placed into one of four vertical forest layer categories: (1) seedlings, all stems less than 1.5 m height; (2) understory, all stems $\geq$1.5 m, but not in a canopy dominant or codominant position; (3) codominant, all stems within the canopy that were not restricted vertically, but crowded on the sides; and (4) dominant, all stems within the canopy that were not restricted vertically and with crowns extended in the main canopy layer. Additionally, the diameter at breast height (dbh) of all stems $\geq$4 cm was measured. Each stem $\geq$4 cm dbh was grouped into one of four diameter classes following Hart and Shankman (2005). In each stand, we noted species that shared canopy positions with eastern hemlock based on visual observation.

Our survey of additional stream reaches yielded one eastern hemlock stand (in Walker County) that was not described by Hart and Shankman (2005) and has not been described elsewhere in the literature. In our analyses, we grouped two eastern hemlock stands in Jefferson County that occurred in such close proximity to each other that we thought they would be best described as a single stand. For these two stands, we combined the 2003 data as well. We used several methods to evaluate decadal changes in these disjunct eastern hemlock stands. The number of eastern hemlock stems in each of the four vertical strata was compared and percent changes were calculated between the 2003 and 2013 censuses. We also compared the number of stems in each of the four diameter classes and calculated the percentage change in each size class between the 2003 and 2013 censuses. In addition, we calculated mean annual temperature, mean annual precipitation, and mean monthly Palmer Drought Severity Index (PDSI) from 2000 to 2013 for our study area available from the National Climate Data Center (2014). We used divisional data with the Upper Coastal Plain National Oceanic and Atmospheric Administration Climate Division (Division 3) of Alabama rather than single-station data, because our study stands spanned three counties.

RESULTS AND DISCUSSION

Eastern Hemlock Stem Abundance

In 2003, the number of eastern hemlock stems in a single stand ranged from 28 to 325 (Figure 2). The 2013 census revealed similar results, as the frequency ranged from 30 to 313 eastern hemlock stems in a single stand. A broad-scale geographic pattern evident in our results was an apparent increased eastern hemlock stem density over the 10-yr observation period in the Fayette County stands, and an apparent decreased stem density of the stands in Walker and Jefferson counties. Based on observational evidence, we were not able to hypothesize specific drivers of eastern hemlock stem density patterns, as they may have been a function of stand-scale processes rather than broad-scale processes (e.g., climate). The effects of stand-scale processes (i.e., stand dynamics) are superimposed over landscapes and regions (i.e., processes common to all stands).

Vertical Structure

Species which commonly cooccurred with eastern hemlock in the canopy of the inventoried stands included white oak (*Quercus alba* L.), American beech (*Fagus grandifolia* Ehrh.), chestnut oak (*Quercus montana* Willd.), northern red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), and tulip poplar (*Liriodendron tulipifera* L.). The most common species in the understory included American holly (*Ilex opaca* Aiton), mountain laurel (*Kalmia latifolia* L.), eastern red cedar (*Juniperus virginiana* L.), bigleaf magnolia (*Magnolia macrophylla* Michx.), and flowering dogwood (*Cornus florida* L.). The understory strata of the stands were

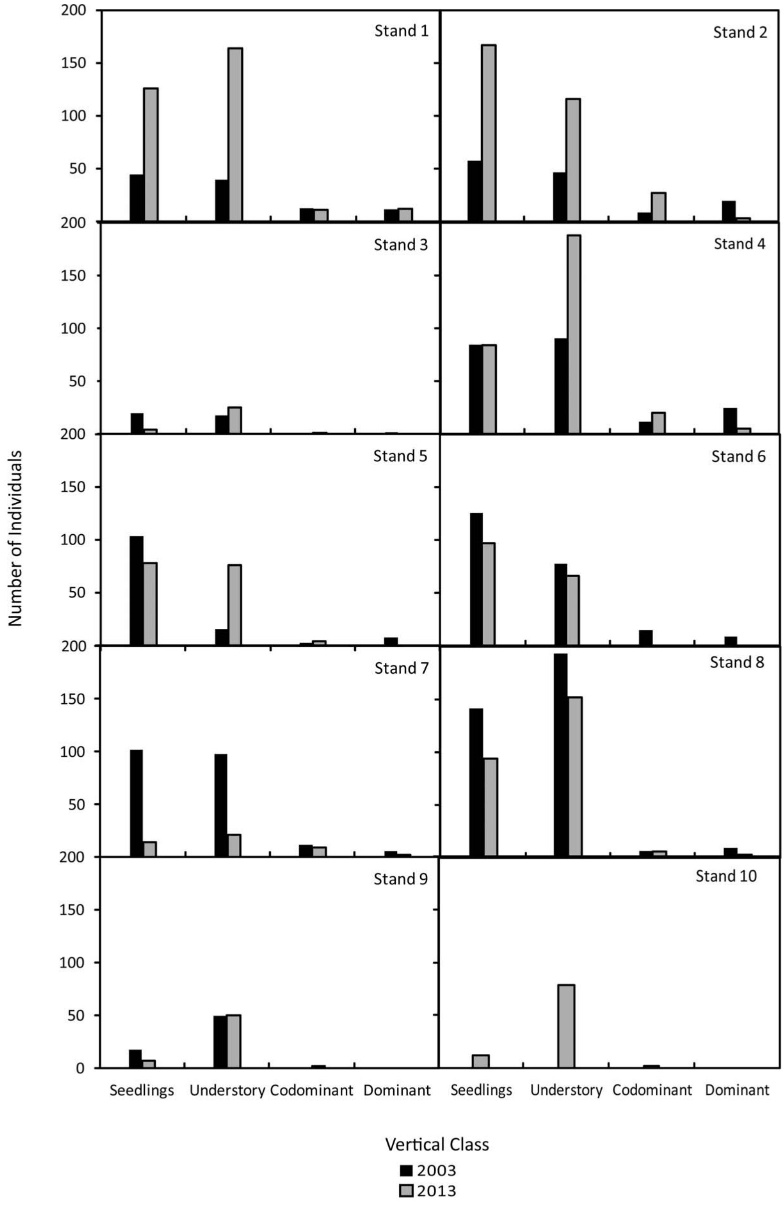

Figure 2. Vertical class distributions of eastern hemlock stems in all sampled stands from the 2003 and 2013 surveys on the Cumberland Plateau, Alabama.

relatively sparse and lacking in woody species, which is characteristic of eastern hemlock stands throughout much of its range (Hadley 2000). Sparse understories in these stands may be attributed to the shade cast by the dense and deep eastern hemlock canopies and the low soil pH in eastern hemlock stands (Finzi et al. 1998, Ellison et al. 2005).

In all 10 stands, eastern hemlock occurred in more than one vertical stratum (Figure 2) and, in half of the sampled stands, eastern hemlock occurred in all vertical classes. Notably, only two stands did not have an eastern hemlock stem in a canopy position at the time of our 2013 sampling. In general, eastern hemlock stems were most abundant in the seedling and understory layers, and the number of individuals in canopy positions was relatively low. Interestingly, the number of eastern hemlock stems in the understory stratum exceeded the frequency of seedlings in 7 of the 10 stands. Decadal changes in vertical structure varied by stand (Figure 3). Of the 9 stands analyzed for 10-yr changes, 6 exhibited increased frequency of individuals in at least 1 vertical stratum and a decreased frequency of eastern hemlock stems in at least 1 vertical class. Only three stands (stands 6, 7, and 8) experienced a decrease in stem frequency in all vertical strata. Stands 6 and 8, however, retained a relatively high frequency of stems in the understory. All but two stands (stands 1 and 2) experienced a decrease of eastern hemlock seedlings between the 2003 and 2013 censuses. This pattern may be attributed to mortality of eastern hemlock individuals in the seedling layer or by recruitment of stems to greater vertical positions. The number of understory stems increased in stands 3, 4, and 5; thus, the decline in seedlings on these sites may be attributed to recruitment to the understory vertical class rather than seedling mortality combined with a lack of eastern hemlock germination.

Dominant canopy individuals decreased in all but two stands (stands 1 and 9), and these dominant individuals likely contribute to the majority of seed production. Cone production in the species typically begins between 20 and 40 yr of age (Hough 1960, Ruth 1974, Goerlich and Nyland 1999). Eastern hemlock typically produce large seed crops every 2–3 yr (Hett and Loucks 1976, Rooney and Waller 1998), but seed viability is relatively low (Godman and Lancaster 1990). Successful reproduction of eastern hemlock is strongly tied to the suitability of the seedbed (Friesner and Potzger 1944, Bormann and Platt 1958). Germination of eastern hemlock seed is facilitated by coarse woody debris, such as logs, that are in advanced states of decay, as well as other substrates, such as mosses (Friesner and Potzger 1944, Bormann and Platt 1958, Brown et al. 1982, Mladenoff and Stearns 1993, Rooney and Waller 1998). The substrate is particularly important in stands with sparse understories (Godman and Lancaster 1990). Eastern hemlock seedlings are typically shallow rooted and, as such, are susceptible to moisture stress (Godman and Lancaster 1990, Mladenoff and Stearns 1993).

Regeneration of eastern hemlock is typically considered to be episodic and to occur when good seed crops coincide with cool and/or wet conditions such that moisture stress is reduced (Bormann and Platt 1958). In the 2003 survey, Hart and Shankman (2005) noted relatively high frequencies of stems in the seedling height class. In the resurvey of 2013, we noted relatively high frequencies of stems in the understory category. We speculated that this pattern was a function of recruitment into the understory height class of the establishment pulse that began about 2003. We hypothesized that the 2003 sampling captured this establishment pulse, which was the result of a good seed crop that coincided with cool, moist conditions. The average annual temperature of 2003 was low, annual precipitation was high, and the PDSI value was high, indicating an adequate supply of moisture, which was critical to establishment and recruitment of eastern hemlock seedlings (Figure 4). Furthermore, the loss of some canopy trees in these stands should have resulted in canopy gaps that provided the opportunity for stems to move from seedling to understory height classes (Kincaid and Parker 2008).

Diameter Structure

In 2003, the diameter structure of all but stand 9 revealed a reverse J-shaped curve. The reverse J-shaped diameter structure indicates a regenerating stand (Nyland 1996). The diameter structure of stand 9 became more unimodal between 2003 and 2013, with an apex in the 4–20-cm dbh class (Figure 5). In 2003, stand 7 exhibited a reverse J-shaped diameter distribution, but eastern hemlock stems at the time of the 2013 sampling occurred evenly across the four size classes. Stand 10 exhibited an apex of eastern hemlock stems in the 4–20-cm dbh class. In fact, the diameter distributions of stands 7 and 9 were similar. Hart and Shankman (2005) found that diameter and age were significantly and positively correlated in these eastern hemlock stands. Thus, based on the diameter structure, we speculate that these two stands may have had similar development and disturbance histories. We also note that the diameter classes used in our study were selected to make direct comparisons to Hart and Shankman (2005), and different distributions may be revealed by changing the size class bins (Nyland 1996).

The major changes in stem density across size classes were all positive (Figure 6). Only stands

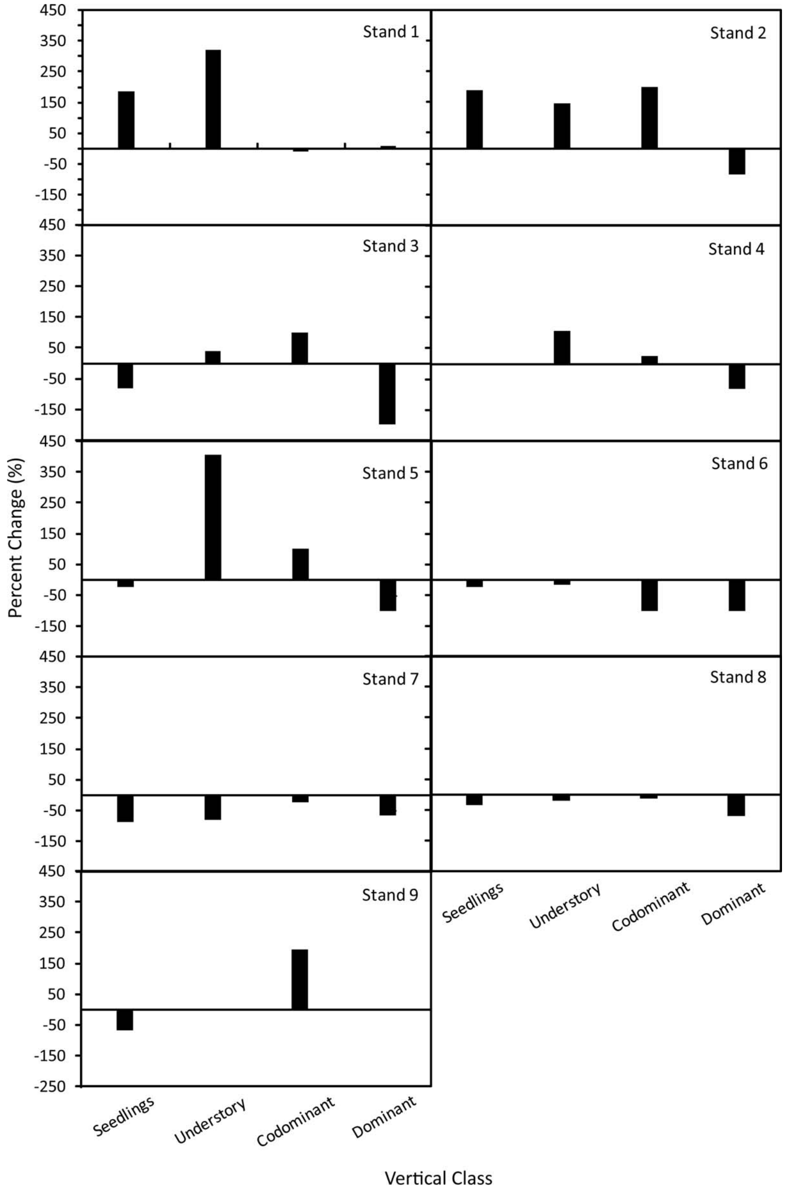

Figure 3. Percent change in the number of eastern hemlock stems in vertical size classes between the 2003 survey and the 2013 resurvey on the Cumberland Plateau, Alabama.

5 and 7 revealed a decrease in the number of stems in the 4–20-cm dbh class, and the changes were relatively minor. In contrast, stands 1, 3, 4, and 8 revealed relatively large increases in the number of stems in this size class. The increase of this particular class (4–20 cm) across most of the stands was likely caused by ingrowth of seedlings that recruited to the larger class combined with a lack of outgrowth of stems from this class to the next. Notably, no stands exhibited an increase in the number of eastern hemlock stems ≥40 cm dbh. The soils of the sites were shallow and the slopes were generally steep. Many of the trees grew out of cracks in the bedrock and had exposed root networks. Thus, these larger stems may be highly susceptible to

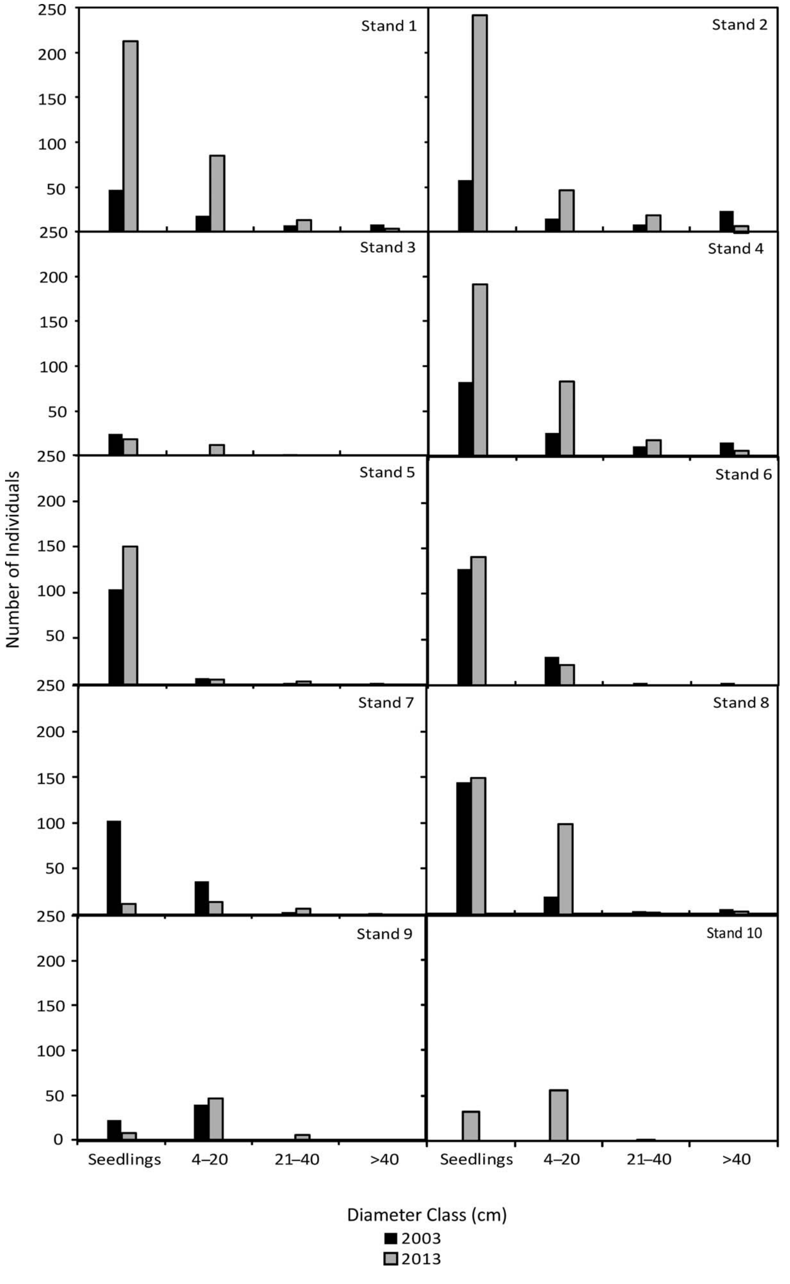

Figure 4. Diameter distributions of eastern hemlock stems in all sampled stands from the 2003 and 2013 surveys on the Cumberland Plateau, Alabama.

windthrow. Hart and Shankman (2005) hypothesized that the biophysical conditions of these sites may limit the size of eastern hemlock stems that can be supported.

The loss of individuals in the >40 cm diameter class may be related to region-scale climatic conditions, more localized weather events, or the senescence of larger and older stems. In 2007, a severe drought affected the region (average monthly PSDI = –3.6; Figure 4), which may have caused water stress–induced mortality, as eastern hemlock stands at the southern

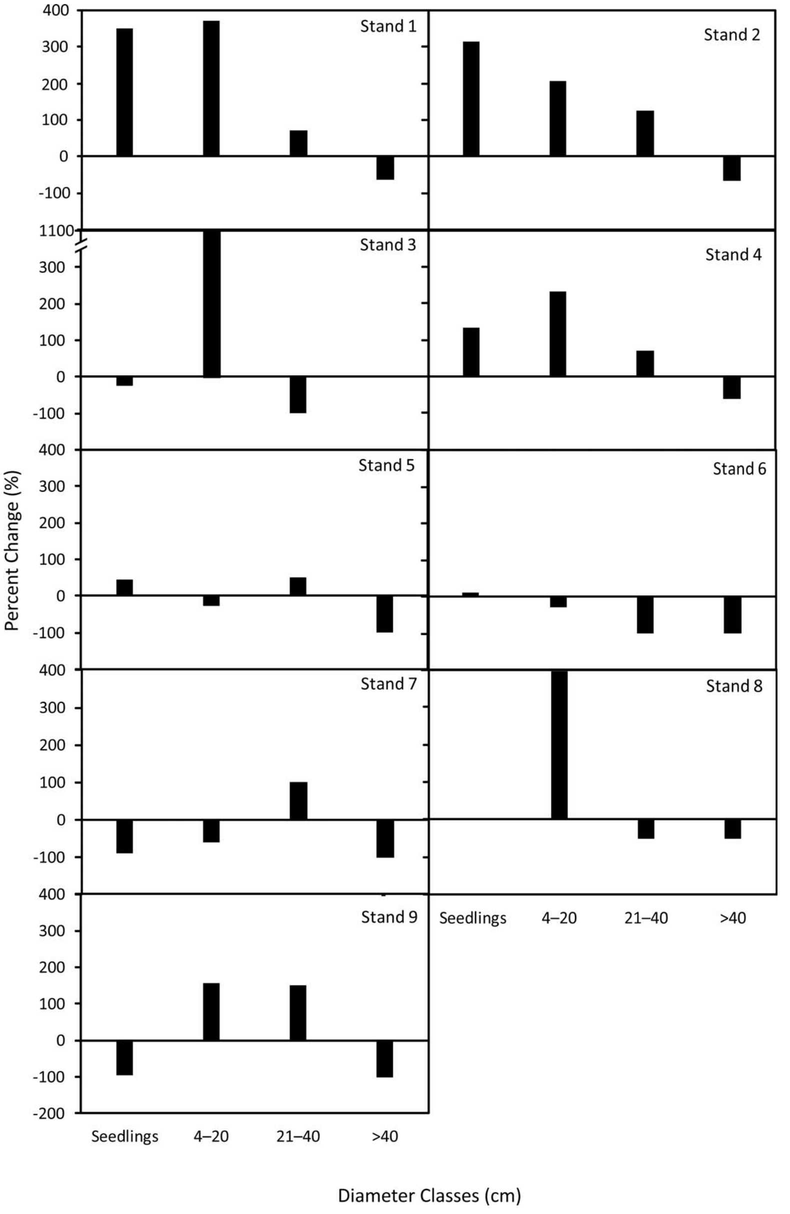

Figure 5. Percent change in the number of eastern hemlock stems in diameter classes between the 2003 survey and the 2013 resurvey on the Cumberland Plateau, Alabama.

boundary of its range are moisture sensitive (Kessell 1979, Hart et al. 2010). These stands may be particularly sensitive, given that they occur on sites that support thin soils that have relatively low moisture-holding capacities and large areas of exposed bedrock.

SUMMARY Although eastern hemlock stem frequency remained relatively constant from 2003 to 2013, stem frequency in the canopy and seedling strata generally decreased. The decrease in eastern hemlock seedlings may be attributed to regional climatic variations that

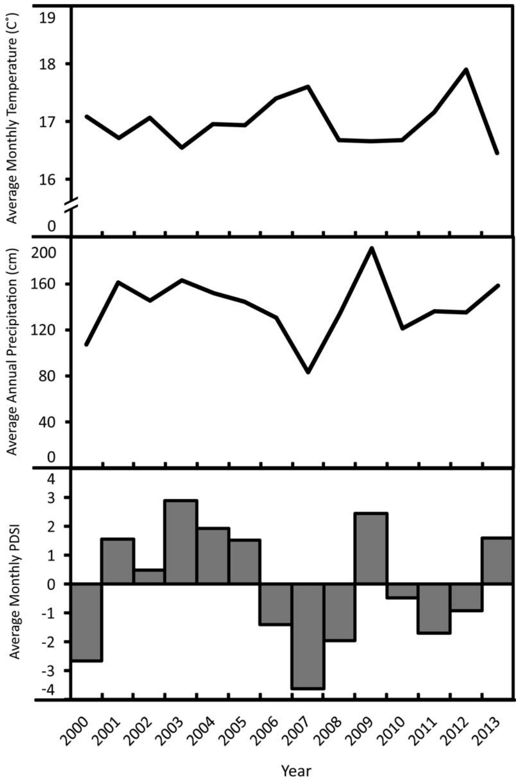

Figure 6. Regional climate characteristics, including average annual temperature, average annual precipitation, and average monthly Palmer Drought Severity Index (PDSI) from 2000 to 2013. All data were obtained from the National Climate Data Center (2014).

resulted in a good seed crop during the 2003 sampling year. Many seedlings sampled in the 2003 survey may have been thus recruited into the midstory strata, additionally explaining the decrease in seedling layer stems. The decline in canopy trees may be a function of site conditions that are unsuitable to support large stems with shallow root systems. The decrease in canopy stems may also be attributed to the regional drought in 2007 that may have killed trees growing on the thin soils. These are general trends across all sampled stands, and individual stands exhibited variations over the 10-yr period. Interstand variations may be attributed to differences in disturbance histories and individual site characteristics. Notably, we found a new stand not sampled in the 2003 survey along a reach of Blackwater Creek. We cannot rule out additional disjunct eastern hemlock stands, but we speculate that no additional stands occur farther south than those reported here. Our decadal resurvey indicated that a viable population of eastern hemlock remains at the southern boundary of its range, but we suggest that factors operating at variable spatial scales, such as regional climatic variations, localized weather events, and stand dynamics, resulted in variations in diameter and vertical size distributions. Based on size structure, and therefore age structure (Hart and Shankman 2005), we suggest that each of these stands is viable. Each stand contains sexually mature eastern hemlock stems that are producing viable seed. Seedlings occur in each disjunct stand and, over the past decade, a recruitment pulse from seedling to sapling size classes was apparent. These stands appear to be regenerating episodically, when good seed crops coincide with cool, moist conditions. As these stands remain reproductively viable, we suggest that the southern range boundary of eastern hemlock is stable and that the external range margin is not currently contracting.

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