Disassociating tree species associations in the eastern United States

Brice B Hanberry

Ecologists have a long history of describing species associations including oak-hickory, one of the predominant associations in the eastern United States. But historically, oak composition did not appear particularly related to hickory composition. I assessed the relevance of the oak-hickory association and other associations using older and recent (c. 1981 and 2007) USDA Forest Service surveys. For common hickory and oak species, I determined percent composition (i.e., percent of total stems ≥12.7 cm in diameter, relative density or abundance) in ecological subsections, changes in composition throughout ranges, and compared composition of oaks and hickories and other potential associations using correlation and ordination. Oaks were among the most abundant species while hickories were minor species. Hickory composition was stable while the trajectory of oak continued to decrease during the survey intervals from presettlement dominance. Rank-order correlation between oaks and hickories throughout their ranges was the maximum as for other species (0.55 and 0.42 during the two survey periods) and in the Oak-Hickory forest region, correlation between oaks and hickories was 0.04 (older surveys) and 0.16 (recent surveys). Oaks were not associated with hickory in the “oak-hickory” forests of Missouri during the mid-1800s, nor were oaks associated with hickory more recently beyond correlations that occur between other eastern forest species. Oak-hickory association in particular is not an informative term for either historical open oak ecosystems or current eastern broadleaf forests. Mixed mesophytic associations, perhaps not best termed as an association, are eastern broadleaf forests where many tree species dominate forested ecosystems in the absence of filtering disturbance. Associations, even if species share similar traits, generally are not strong, stable in time, or extensive in space; differences between species result in different and changing distributions in response to the environment, land use, disease, and other influential factors.

Keywords: Eastern Broadleaf Forests, Mixed Mesophytic, Oak-hickory, Southern Mixed Forests, Sugar Maple-beech

Introduction

Plant ecologists have spent well over a century defining plant associations along successional pathways (Pound & Clements 1898, Schmelz & Lindsey 1970). Clements (1936) influenced plant classifications in both the United States and Great Britain.

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Fig. 1 - The Northern Mixed Forest (warm continental division shaded black), Eastern Broadleaf Forest (hot continental division shaded in darker gray colors and striped), and Southern Mixed Forest (subtropical division shaded in lighter gray colors and white) regions of the United States (ECOMAP 1993, USDA Forest Service). The Eastern Broadleaf Forest is divided into an “Oak-Hickory” forest region, a Maple-Beech-Basswood forest region, and a Mesophytic forest region, following Braun (1950). The Southern Mixed Forest is divided into three ecological provinces of Outer Coastal Plain Mixed Forest, Southeastern Mixed Forest, and Lower Mississippi Alluvial Valley.

Fig. 2 - Change in percent composition of hickory (upper panel) and oak (lower panel) ranges (five most common species combined).Outlined ecological subsections represent current range (% composition ≥0.5).
souri Ozarks includes some riverine ecological subsections (Fig. 2 displays ecological subsections), where oak was 10 to 15% of composition, and conversely, in two subsections oaks were 95% of composition. In contrast, all combined hickory records were 5.5% of total composition. In four ecological subsections, hickory reached 8% to 10% of composition, and hickories were the most abundant after oaks where shortleaf pine was not present. However, the hickory genus in Missouri consists of the five common hickory species, and a few more species in addition, and thus each species probably contributed no more than 5% of composition. Based on imbalanced composition, it seems more reasonable to label these forest types as oak or by dominant species of oak rather than as oak-hickory. Moreover, in the Missouri Ozarks, rank-order correlation between percent composition of the two genera was -0.09 and inclusion of all Missouri resulted in a correlation of -0.17 (B. Hanberry, unpublished data).

Given the lack of any particular balance or correlation between oak and hickory composition historically and differing dynamics and traits between the genera, I evaluated the validity of oak-hickory associations at large extents, including their ranges in the eastern US (Fig. 1), using the oldest USDA Forest Service Forest Inventory and Analysis (FIA) surveys and the most recently completed cycles. Associations should be composed of species that are dominant, whether by coverage, density, or biomass, and additionally, associated species should share similar traits, resulting in similar changes in composition in response to the environment. Do oaks and hickories have dominant composition and share compositional trajectories throughout oak and hickory ranges or in Braun’s Oak-Hickory forest region (Fig. 1)? If oaks were not associated by correlation with hickory in the “oak-hickory” forests of Missouri during the mid-1800s, were oaks associated by correlation or ordination with hickory more recently throughout oak and hickory ranges or in the Oak-Hickory forest region specified by Braun (1950)? Is there a strong association between any eastern forest species, for example oak-red maple (Acer rubrum) or oak-pine or sugar maple (Acer saccharum) -American beech (Fagus grandifolia) or red spruce (Picea rubens)-balsam fir (Abies balsamea)?

**Methods**

The USDA Forest Service Forest Inventory and Analysis (FIA DataMart, [http://www.fia.fs.fed.us/tools-data](http://www.fia.fs.fed.us/tools-data)) records data from long-term forest plots located about every 2000-2500 ha across the country. Each plot contains four 7.3 m radius subplots, arranged as a central subplot surrounded by three outer subplots. Starting in 1999, plot designs and inventory cycles became standardized, with 20% of plots measured each year in the eastern US. Small trees <12.7 cm in diameter are sampled in smaller areas within subplots and thus, I limited the study to trees ≥12.7 cm in diameter.

From the eastern US regions (warm continental, hot continental, and subtropical divisions - ECOMAP 1993; Fig. 1), I selected the most recently completed cycles, ranging from 2001 to 2012 (mean = 2007, SD = 2.2) and the oldest surveys, ranging from 1968 to 1995 (mean = 1981, SD = 7.6). I retained ecological subsections that matched spatially between the oldest surveys and most recent cycles. Ecological subsections are the smallest ecological unit provided in FIA surveys (mean area = 700,000 ha, SD = 6.82,000 - ECOMAP 1993; Fig. 2). I calculated percent composition (i.e., percent of total stems; adjusted for diameter bias present in variable radius plot sampling in older surveys) for all plots combined in each ecological subsection to determine dominance and changes in percent composition to assess trajectories for combined hickories and oaks, and other common species, by ecological regions and provinces, modified to better match Braun’s forest regions. I mapped ranges (≥0.5% of total species composition in ecological subsections to exclude transient presence or recent naturalization or plantings outside of ranges that may not become permanent) and changes in range, to examine trajectories in composition spatially. Because unidentified hickories in older surveys became identified in current surveys, I combined the most common five species of each genus and assigned all of the unknown hickory species to the five most common hickory species, which accounted for 95% of hickory stems. The five most common oak species accounted for 65% of oak stems.

I used Spearman rank-order correlation analysis ([Proc. Corr](http://www.sas.com/software/sas)), SAS software, version 9.1, to assess correlations between oak and hickory composition across the region. Spearman rank correlation coefficients were used due to the non-parametric nature of the data. I used a significance level of α ≤ 0.05 and assumed normal distribution and homogeneity of variance between the groups.

I used *F* tests to assess differences in composition among ecological subsections. I used Tukey’s honestly significant difference (HSD) tests to assess differences among ecological subsections post hoc. I used the SAS software, version 9.1, to calculate these tests.

### Tab. 1 - Compositional percent (percent of total stems ≥12.7 cm in diameter) of common hickory and oak species and relevant species in older (approximately 1984 for each genus) and recent (approximately 2007) FIA surveys by ecological province (ECOMAP 1993) and forest region (Braun 1950).

<table>
<thead>
<tr>
<th>Province/Forest Region</th>
<th>Genus or species</th>
<th>Older (%)</th>
<th>Recent (%)</th>
<th>Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Midwest Broadleaf Forest/Sugar maple-basswood-beech</td>
<td>hickory</td>
<td>4.47</td>
<td>4.66</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>oak</td>
<td>16.15</td>
<td>11.17</td>
<td>-4.98</td>
</tr>
<tr>
<td></td>
<td>American basswood</td>
<td>3.99</td>
<td>4.24</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>American beech</td>
<td>0.65</td>
<td>0.58</td>
<td>-0.07</td>
</tr>
<tr>
<td></td>
<td>sugar maple</td>
<td>4.36</td>
<td>5.26</td>
<td>0.90</td>
</tr>
<tr>
<td>Eastern, Appalachian, and eastern Central Interior</td>
<td>hickory</td>
<td>8.32</td>
<td>7.34</td>
<td>-0.98</td>
</tr>
<tr>
<td>Broadleaf Forest/Mesophytic</td>
<td>oak</td>
<td>30.13</td>
<td>24.33</td>
<td>-5.80</td>
</tr>
<tr>
<td></td>
<td>American basswood</td>
<td>0.52</td>
<td>0.59</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>American beech</td>
<td>1.63</td>
<td>1.83</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>pines</td>
<td>9.87</td>
<td>7.70</td>
<td>-2.16</td>
</tr>
<tr>
<td></td>
<td>red maple</td>
<td>7.44</td>
<td>10.69</td>
<td>3.25</td>
</tr>
<tr>
<td></td>
<td>sugar maple</td>
<td>3.95</td>
<td>4.75</td>
<td>0.80</td>
</tr>
<tr>
<td></td>
<td>tuliptree</td>
<td>4.38</td>
<td>4.88</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>yellow buckeye</td>
<td>0.06</td>
<td>0.25</td>
<td>0.20</td>
</tr>
<tr>
<td>Western Central Interior Broadleaf Forest, Arkansas</td>
<td>hickory</td>
<td>11.19</td>
<td>11.04</td>
<td>-0.16</td>
</tr>
<tr>
<td>Ozarks and Ouachita and Valley/Oak-Hickory</td>
<td>oak</td>
<td>47.45</td>
<td>39.78</td>
<td>-7.67</td>
</tr>
<tr>
<td>Southeastern Mixed Forest</td>
<td>hickory</td>
<td>4.54</td>
<td>3.66</td>
<td>-0.88</td>
</tr>
<tr>
<td></td>
<td>oak</td>
<td>12.17</td>
<td>9.40</td>
<td>-2.77</td>
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<tr>
<td>Outer Coastal Plain Mixed Forest</td>
<td>hickory</td>
<td>1.24</td>
<td>0.71</td>
<td>-0.53</td>
</tr>
<tr>
<td></td>
<td>oak</td>
<td>3.58</td>
<td>2.05</td>
<td>-1.53</td>
</tr>
<tr>
<td>Lower Mississippi Alluvial Valley</td>
<td>hickory</td>
<td>2.41</td>
<td>2.29</td>
<td>-0.12</td>
</tr>
<tr>
<td></td>
<td>oak</td>
<td>3.99</td>
<td>2.82</td>
<td>-1.18</td>
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9.1, Cary, NC, USA) to statistically compare composition. I also correlated composition in the Oak-Hickory forest region (Fig. 1). I examined other correlations with oaks, including a common pine genus (excluding commercial pines such as loblolly, *Pinus taeda*) and other common species, as well as correlations among sugar maple-American beech-eastern hemlock (*Tsuga canadensis*) and red spruce-balsam fir associations. I also used non-metric multidimensional scaling (NMS) ordination to represent species composition along axes based on the Sørensen/Bray-Curtis distance measure (“ecodist” package in R - Goslee & Urban 2007).

**Results**

In the Eastern Broadleaf Forest region, the five most common oak species combined were 27% of composition in older surveys and declined to 22% of composition in more recent surveys. Four of the five oak species contributed 4% to 7% of composition, and thus, oaks were among the most abundant species, in the following order of decreasing abundance: red maple, white oak, sugar maple, chestnut oak, yellow-poplar, northern red oak, and black oak. The five most common hickory species combined were 7% to 8% of composition during both survey intervals. Pignut hickory was the most common species at 2% of composition.

By ecological province/forest region, oak composition also declined while hickory composition remained relatively stable. Indeed, in Braun’s Oak-Hickory forest region, oaks declined from 48% to 40% of composition, while hickories were about 11% of composition during both survey intervals (Tab. 1). Similarly, hickory composition throughout its range overall was stable relative to oak (Fig. 2).

Throughout the eastern US, rank-order correlation values in general were weak (<0.4 - Tab. 2 and Tab. 3). After butternut (*Juglans cinerea*), hickories had the greatest correlations with oaks, of *r = 0.55* in older surveys and *r = 0.42* in more recent surveys. In the Oak-Hickory forest region, correlation between oaks and hickories was 0.04 (older surveys) to 0.16 (recent surveys) and not significant. Correlations between sugar maple and American beech were 0.52 in older surveys and 0.42 in recent surveys. Beech had

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**Tab. 2** - Significant correlations ≥ 0.4 among oak (five most common species), hickory (five most common species), pine (excluding commercial pine species), and red maple. (n/a): not applicable.

<table>
<thead>
<tr>
<th>Survey</th>
<th>Species/genus</th>
<th>Oaks</th>
<th>Hickories</th>
<th>Pines</th>
<th>Red maple</th>
<th>P-value oaks</th>
<th>P-value hickories</th>
<th>P-value pines</th>
<th>P-value red maple</th>
</tr>
</thead>
<tbody>
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<td>Older surveys</td>
<td>oaks</td>
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<td>0.55</td>
<td>0.20</td>
<td>-0.08</td>
<td>n/a</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>0.15</td>
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<td></td>
<td>butternut</td>
<td>0.57</td>
<td>0.28</td>
<td>-0.89</td>
<td>-0.44</td>
<td>0.05</td>
<td>0.43</td>
<td>0.01</td>
<td>0.18</td>
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<tr>
<td></td>
<td>hickories</td>
<td>0.55</td>
<td>1.00</td>
<td>-0.06</td>
<td>-0.29</td>
<td>&lt;0.01</td>
<td>n/a</td>
<td>0.37</td>
<td>&lt;0.01</td>
</tr>
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<td>scarlet oak</td>
<td>0.49</td>
<td>0.09</td>
<td>0.21</td>
<td>0.01</td>
<td>&lt;0.01</td>
<td>0.33</td>
<td>0.03</td>
<td>0.94</td>
</tr>
<tr>
<td></td>
<td>sourwood</td>
<td>0.48</td>
<td>0.02</td>
<td>0.12</td>
<td>0.48</td>
<td>&lt;0.01</td>
<td>0.93</td>
<td>0.52</td>
<td>0.01</td>
</tr>
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<td></td>
<td>yellow-poplar</td>
<td>0.47</td>
<td>0.30</td>
<td>-0.07</td>
<td>0.25</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>0.40</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>blackjack oak</td>
<td>0.42</td>
<td>0.00</td>
<td>0.16</td>
<td>-0.26</td>
<td>0.01</td>
<td>0.99</td>
<td>0.35</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>eastern redec</td>
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<td>0.39</td>
<td>-0.24</td>
<td>-0.07</td>
<td>0.99</td>
<td>&lt;0.01</td>
<td>0.02</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>eastern hemlock</td>
<td>-0.05</td>
<td>-0.53</td>
<td>0.25</td>
<td>0.50</td>
<td>0.64</td>
<td>&lt;0.01</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
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<td>-0.31</td>
<td>1.00</td>
<td>0.15</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td>black cherry</td>
<td>-0.09</td>
<td>-0.16</td>
<td>-0.25</td>
<td>0.44</td>
<td>0.18</td>
<td>0.04</td>
<td>0.00</td>
<td>&lt;0.01</td>
</tr>
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<td>red mulberry</td>
<td>-0.36</td>
<td>-0.30</td>
<td>0.24</td>
<td>0.51</td>
<td>0.09</td>
<td>0.17</td>
<td>0.44</td>
<td>0.03</td>
</tr>
<tr>
<td>Recent surveys</td>
<td>oaks</td>
<td>1.00</td>
<td>0.42</td>
<td>0.11</td>
<td>-0.05</td>
<td>n/a</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>butternut</td>
<td>0.54</td>
<td>-0.24</td>
<td>-0.41</td>
<td>-0.75</td>
<td>&lt;0.01</td>
<td>0.42</td>
<td>&lt;0.01</td>
<td>0.01</td>
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<tr>
<td></td>
<td>blackjack oak</td>
<td>0.48</td>
<td>0.21</td>
<td>0.18</td>
<td>-0.32</td>
<td>&lt;0.01</td>
<td>0.02</td>
<td>&lt;0.01</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>hickories</td>
<td>0.42</td>
<td>1.00</td>
<td>-0.06</td>
<td>-0.24</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>0.02</td>
<td>0.01</td>
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</table>
slightly stronger correlations with yellow birch and significant but weak correlations with eastern hemlock. Correlation between red spruce and balsam fir in both surveys was about 0.75 and significant. Ordinations, which account for similar values in composition, did not show that oak and hickory were more similar than oak and pine in either the eastern US or Oak-Hickory forest region (Fig. 3 and Fig. 4).

**Discussion**

Associations, even if significant, generally are not strong or stable. Associations are difficult to define consistently in space and time, particularly as spatial and temporal scales increase (Gleason 1926). Although correlation values between the most common oak and hickory species increased from historical forests of Missouri, which contributed the major extent of Braun’s Oak-Hickory forest region, during the mid-1800s to current forests, it values (i.e., 0.42 to 0.55) and ordinations did not show particular association between oaks and hickories. Ranges of the common oaks and hickories were similar, but otherwise oak composition was about three times as great as hickories and hickory composition was stable while the trajectory of oak continued to decrease from presettlement dominance.

When oak-hickory forest associations were described in the late 1800s, there may have been a greater compositional balance and spatial association of oak to hickory. Extensive harvest of interior eastern forests, which probably were open oak ecosystems where oaks dominated in the presence of frequent surface fires, occurred rapidly during approximately 1880-1920 due to advances in industrialization (Hanberry et al. 2014a, but see Matlack 2013). Generally, harvest was somewhat selective based on economics to provide certain species and size classes to sawmills; dominant, large diameter oaks probably were the first tree removals. After forest harvest, effective fire suppression began about 1920. Although lack of disturbance initially favored dominant oak trees that were present and regenerating, ultimately, lack of fire allowed colonizing, fire-sensitive species to remain established (but see Matlack 2013). Forests increased in stem density, but oaks lost ground compared to numerous fire-sensitive species and are now 55% of the Missouri Ozarks (Hanberry et al. 2014a). Hickories were not particularly favored by fire and have increased in the Missouri Ozarks to 11% of composition.

Perhaps when oak declines to composition levels similar to hickory, correlation will increase, despite differences in life history traits. Nevertheless, it is not informative to name a forest ecosystem type based on two genera with composition no greater than numerous species or genera that are present.
Rather, this type of association is termed “mixed mesophytic”, or an association of nume-
rous species (>20 species of many genera - Braun 1935). Mixed mesophytic associa-
tions are diverse forests composed of varying species with no particular dominance or
shared traits, aside from tolerance to current land use. Mixed mesophytic forests in the
central eastern United States, where nume-
rous broadleaf species are present, may be
more typically named by location, composi-
tion, and vegetation state as eastern broad-
leaf forests, with “mixed” reserved for mix-
tures of broadleaf and needled species rather
than a mixture of species (ECOMAP 1993 -
Fig. 1).

Mixed mesophytic forests currently are
composed of species that historically were
limited to sites protected from disturbance,
which filtered species by traits. Historical
disturbances otherwise created alternative
states, for example, open oak or pine ecosys-
tems in ecological provinces where there was
frequent fire disturbance (but see Matlack
2013) or floodplain forests where there was
flooding disturbance. Mesic sites are not as
important for “mesophytic” species as dis-
turbance-free areas, except in sites of ex-
reme moisture stress in very xeric or hydric
soils (Hanberry et al. 2012a). The stress of
fire and flooding removes establishment of
colonizing fire-sensitive and flooding-sensi-
tive species. When species are released from
disturbance stress because of fire suppres-
sion and flooding regulation, a wide range of
disturbance-sensitive species establish and
eventually dominate areas where there used
to be an active disturbance regime. Current-
ly, in areas where urbanization and forestry
are major land uses, moderately shade-toler-
ant species such as red maple (see Tab. 1) are
most abundant and in areas where inten-
sive agriculture is the major land use, species
that are tolerant to exposure are more abund-
(dant (Hanberry et al. 2014b).

Other widespread associations in the Uni-
ted States include sugar maple-American
beech that developed over hundreds of years
without disturbance. There appears to be
evidence from historical records that sugar
maple-beech was a more representative asso-
ciation than oak-hickory because both sugar
maple and beech were dominant and long-
lived species with similar traits that represent
forests after long periods without distur-
bance, perhaps a true “climax” association
(Seischab 1990, Fuller et al. 1998, Bürgi et
al. 2000, Lorimer 2001, Cogbill et al. 2002,
Whitney & DeCant 2003, Wang et al. 2010,
Thomas-Van Gundy & Strager 2012). Addi-
tionally, in the northern lower peninsula of
Michigan, historical rank-order correlation
was 0.87 (B. Hanberry, unpublished data).
Nevertheless, the association was not con-
sistent throughout the eastern US because
the two species have different distributions.

American beech range extends south to Me-
xico and used to extend across the country,
but now is more limited than sugar maple
range, which extends further west. In the
northeast, eastern hemlock may have had
greater correlation with beech whereas sugar
maple gained other tree associates such as
American basswood in western regions out-
side of current beech distribution (Bürgi et
al. 2000, Cogbill et al. 2002, Whitney & De-
cant 2003). Because long periods without
disturbance by current land use (i.e., tree re-
movals occur more frequently than the life-
span of most tree species) are not present in
the landscape, sugar maple and beech were
not likely to continue as a dominant associa-
tion; instead, current correlation between the
two species was not particularly strong and
American beech currently is a minor species.
Sugar maple has increased whereas beech has
decreased, probably due to multiple fac-
tors including forestry selection against
beech and larger gaps that favors sugar
maple, poor beech dispersal after harvest,
and beech back disease (Cryptococcus fa-
gioga and Neoectria - Dyer 2001, Suffling
et al. 2003). Likewise, the oak-chestnut asso-
ciation of the eastern side of eastern broad-
leaf forests has been disassociated by chest-
nut blight and subsequent preemptive har-
vest that removed potentially resistant geno-
types. At smaller scales, red spruce-balsam
fir may be one of the strongest associations
(r = 0.75) due to shared traits, dominance in
high elevation or latitude distributions, and
similar trajectories.

Conclusions

We have inherited ecological terminology,
some of which may never have been essen-
tial, including association-segregate, conso-
ciation, fasciation, location, formation, as-
ociates, associates-segregate, and developmen-
tal unit (Braun 1935). Oak-hickory associa-
tion, which is still in use, is not descriptive
of either historical open oak ecosystems or
current eastern broadleaf forests. The mixed
mesophytic association additionally may bet-
er align with current terminology by use of
the term broadleaf or even deciduous forest
rather than refer to an association composed
of many species of no particular dominance
or shared traits. Many disturbance-sensitive
species are present in forested ecosystems in
the absence of disturbance, but forest types
of multiple species can be specified by loca-
tion (i.e., eastern, southern, western, nor-
tern) and taxonomy (i.e., broadleaf or need-
led, angiosperm or gymnosperm, or deci-
duous or evergreen, and mixed to indicate
balance between angiosperms and gymno-
spersms rather than a mixture of species - see
Fig. 1). Forest implies a closed state, and in
historical forest ecosystems, the open state
may be incorporated with composition (i.e.,
open oak or pine forest ecosystems).

Although tree species share some overlap-
ning traits and consequently, occupy similar
sites, because of species-specific differences
in traits and general lack of dominance by
two species over a large shared extent, strong
associations probably are limited in time and
space. Additionally, because of dif-
ferring species dynamics in response to dri-
vings factors such as land use and disease, as-
sociations do not persist and consequently, it
is important not to model future forests
based on transitory and weak current associa-
tions, i.e., project future movement by
groups of species, when species will have
different responses to environmental change.
Even though more permanent than associa-
tions, forest ecosystem types also are not
stable; without disturbance, open oak and
pine ecosystems transitioned to closed forest
composed of numerous species that are fire-
sensitive. Mesophytic associations will en-
dure indefinitely, but more simply termed
eastern broadleaf forest in the eastern United
States where angiosperms are dominant.

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