Revisiting the Deciduous Forests of Eastern North America

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Deciduous Forests of Eastern North America, written by E. Lucy Braun and published in 1950, included a map depicting "original" (virgin) forest pattern. Her classification of forest regions remains an influential reference, though it was shaped by ecological assumptions that researchers consider outdated today. In this article, I present a new map of forest regions, using a data set from an extensive network of contemporary forest plots. Although there are differences between the two maps, including the homogenization of forests in the central section of the deciduous forest formation, the geography of Braun's forest regions is largely maintained. The similarities between the maps are noteworthy, considering the methodological differences in their creation and the intensive land use changes, fire suppression, introduction of exotic species, and changes in atmospheric chemistry that have occurred since Braun's work.

Keywords: eastern deciduous forest, E. Lucy Braun, vegetation mapping, forest regions, cluster analysis

Before the arrival of European settlers, forest was the dominant land cover in the eastern United States, extending from New England to Florida and westward to the prairies of the Great Plains (Greeley 1925). Native American communities had certainly influenced forest composition and structure, though the magnitude and extent of their influence are subject to continuing debate (Russell 1983). It was in the 18th and 19th centuries, however, that an unprecedented modification of the forests of the eastern United States took place. Forests were cleared extensively for agriculture, timber production, fuelwood, and urban expansion (Whitney 1994), such that forest cover reached its nadir in the early 20th century. According to US Census records, of the total acreage of land in farms in the eastern United States, less than 10 percent was reported as nonpastured woodland in 1930 (Geospatial and Statistical Data Center 2004). Now this area east of the 100th meridian is nearly 40 percent forest cover (USGS/USFS 2002). So although forest cover has increased dramatically in parts of the eastern United States over the last century, most forest land is successional, and quite distinct from old-growth forests.

Biotic communities are shaped by the interaction of three templates: the physical environment (climate, soils), biotic interactions (competition, predation), and disturbances (fire, windthrow). Over the past 300 years, human activity in the eastern United States has altered all of these templates, resulting in forests that are not only much younger but in many cases dramatically different from the presettlement forest in terms of composition and structure. Numerous studies have detailed the biological consequences of anthropogenic change to the physical environment, including climatic warming (McNulty and Aber 2001), acid rain and other changes in atmospheric chemistry (Driscoll et al. 2001), and altered hydrologic regimes (Magilligan and Stamp 1997, Cowell and Dyer 2002). Biotic interactions have been altered by the introduction of a large and growing number of exotic species that compete with native species, as well as an expanding list of host-specific insects, fungi, and pathogens that may cause significant mortality to particular species within a forest (Rossman 2001), much as the chestnut blight (*Cryphonectria parasitica*) did in the early 20th century. Disturbance regimes have also been altered, decreasing the rate of some disturbances and introducing novel ones. Anthropogenic changes may include the exclusion of natural disturbances—fire, for example—resulting in a decrease in disturbance-adapted species such as pines (Cowell 1998, Radeloff et al. 1999). The introduction of novel disturbances may have even more wide-reaching and dramatic effects. Agricultural clearing, for instance, followed by abandonment and forest regeneration, tends to favor shade-intolerant species, such as the fast-growing tulip poplar (*Liriodendron tulipifera*) or red maple (*Acer rubrum;* Dyer

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2001). Because of the changes to the three templates, and the ensuing interactive effects, contemporary forests may be significantly different from the presettlement forests.

Deciduous Forests of Eastern North America, written by E. Lucy Braun, was recognized soon after its publication in 1950 as a major contribution to plant ecology (Stuckey 1973). Braun's stated goal was to describe the pattern and composition of the "original" (or virgin) forest pattern of eastern North America and the composition of virgin forests. The book includes a map of nine forest regions (see figure 1), which she based largely on her own field sampling of old-growth stands and an extensive review of the literature; a separate chapter is devoted to a discussion of each forest region within the book. Braun defined her forest regions on the basis of physiognomy (overall appearance and structure) and similarities in composition. She believed that climate—for example, growing season length or precipitation effectiveness (the proportion of total precipitation available for plant use)—controls the position of vegetation types relative to each other, but that regional boundaries are determined by historical factors: changing climate and physiography (landforms) of the past. Braun stated that vegetation features were usually the basis of the boundaries she delineated, though physiographic boundaries may have served as forest region boundaries when they were less distinctive.

To this day, Braun's map of forest regions remains one of the most widely referenced classifications of eastern forests, even though it was founded on ecological assumptions that researchers consider outdated today. Braun was influenced by the plant ecologist Frederic Clements, who viewed ecological communities as "superorganisms" that progressed from youth to maturity through a series of species replacements (succession), ultimately converging on a climax community in equilibrium with climate. Clements's (1916) views of succession dominated ecological thinking for decades, despite the criticisms of other early ecologists (Gleason 1926, Watt 1947, Egler 1954). Today, biogeographers and plant ecologists have moved away from the deterministic views espoused by Clements. Stochastic processes such as dispersal and establishment, and especially the role of disturbance, are seen as major shapers of vegetation communities; community ecologists question whether most ecosystems could remain stable over sufficiently long periods of time to enable the vegetation to achieve equilibrium. For example, Braun argued that during the Pleistocene, the most recent glacial period, the deciduous forest south of the ice margin was not displaced south of the glacial boundary (figure 2). Rather, refugia near the ice front made it possible for species to maintain the distribution pattern attained by the close of the Tertiary two million years ago, allowing coevolution and coadaptation of the resident species. Although the existence of refugia near the ice margin is a possibility (McLachlan et al. 2005), palynological evidence does not support this view, suggesting instead that species responded individualistically to climatic changes of the past (Williams et al. 2004).

A new map of eastern US forests

Other vegetation classifications covering the entire eastern United States have been proposed since Braun's 1950 publication. Perhaps most noteworthy is Küchler's (1964) map of
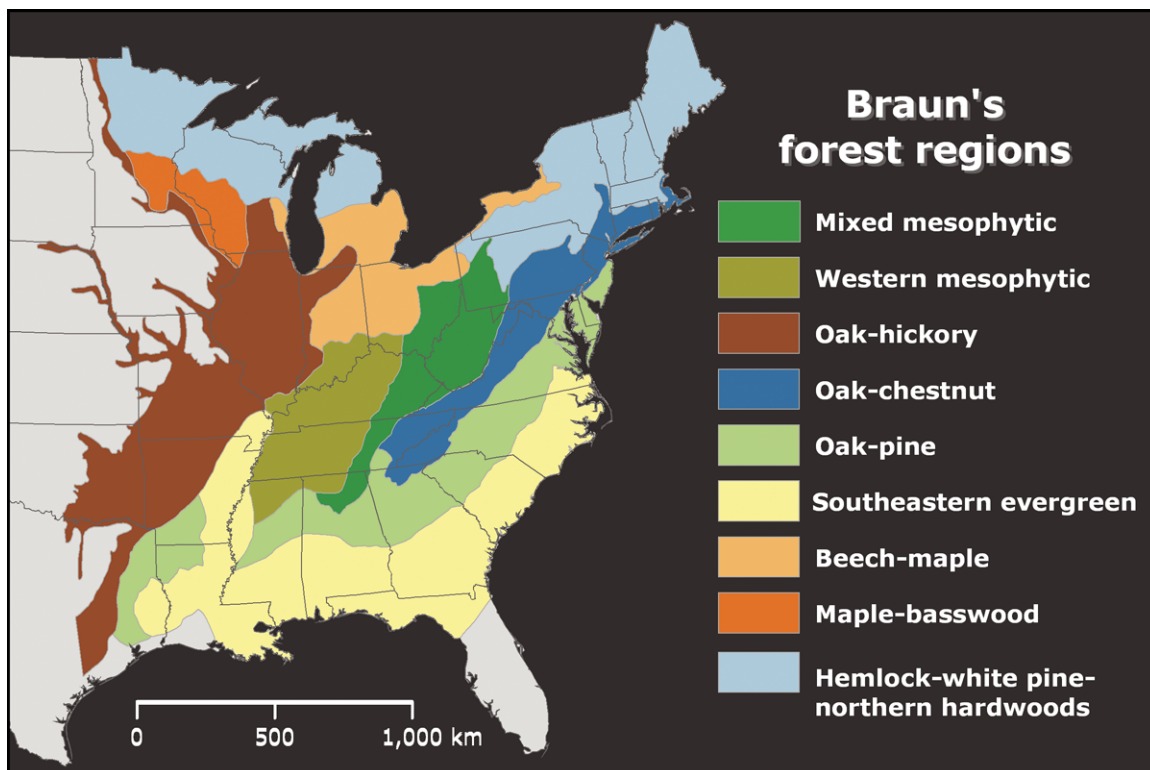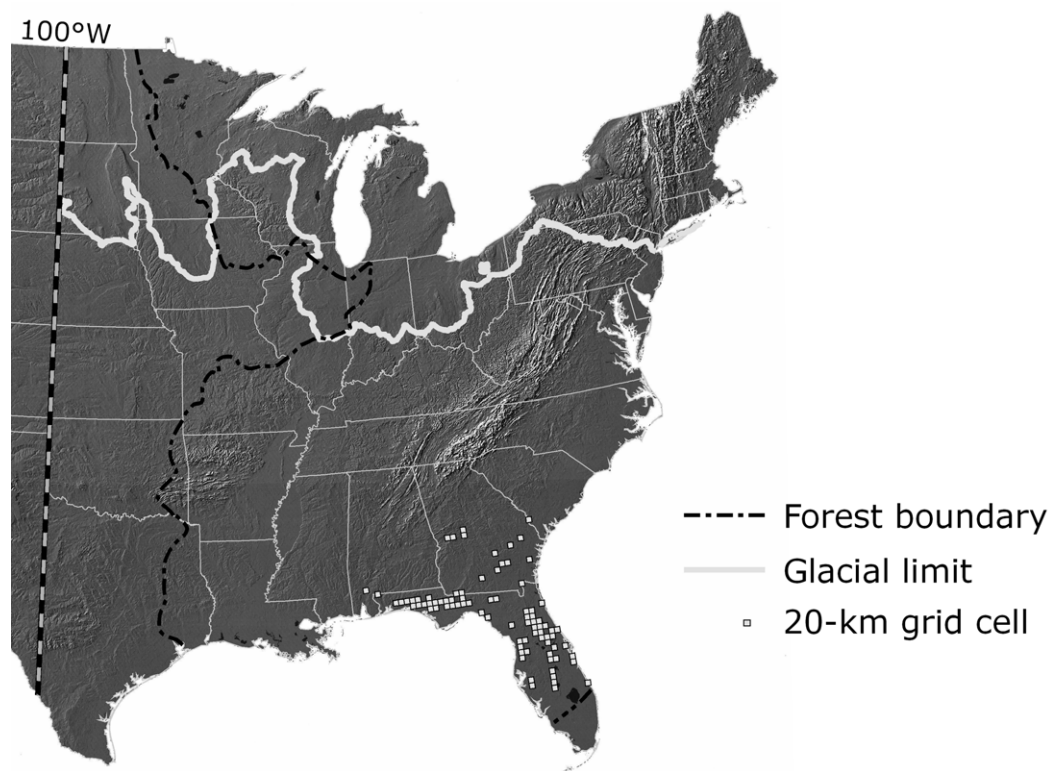

Figure 1. *The nine regions described by Braun (1950), representing original forests of eastern North America.*

*Figure 2. Location map with topography. For illustration, 20-kilometer grid cells are shown that contain sand pine (*Pinus clausa*), a species largely restricted to the subtropical evergreen forest region. Source: Bailey 1995 (forest boundary), Fullerton et al. 2003 (glacial boundary), Thelin and Pike 1991 (shaded relief map), Prasad and Iverson 2003 (Forest Inventory and Analysis grid data).*

"potential" vegetation, which includes 35 categories within the area covered by Braun's map (figure 1). Direct comparison of classifications in the present study and other classifications may be limited by the large number of categories they contain (Eyre 1980) or by the lack of an accompanying map (Monk et al. 1989, Vankat 1990), or both. Additionally, sufficient cartographic generalization may be lacking from some maps, such as more recent classifications of forest cover types derived from satellite imagery (Schmidt et al. 2002). Several maps of "ecological units" or "ecoregions" present a nested hierarchical classification covering the eastern United States (Omernik 1987, Bailey 1995, Keys et al. 1995); however, vegetation is only one of the criteria they use to classify areas. Often these maps use Küchler's classification as a basis for the vegetation component. Despite the many classifications that exist, Braun's map remains a standard for describing deciduous forests of the eastern United States.

In this study I revisit Braun's map, since her classification continues to be an influential reference. Such a reassessment is justified for a number of reasons. First, a reconsideration is valuable in the context of current understanding of the ecological processes shaping contemporary forests, to see if Braun's Clementsian bias affected the delineation of her forest regions. Second, given the extraordinary changes that have taken place within the deciduous forest formation, it is of interest to see if Braun's regions, which she based largely

on old-growth stands, have changed significantly. Finally, Braun's characterization of forest regions was constrained both by her ability to visit the different regions and by the diversity in materials previously published on them. Today, researchers have access to a large and geographically extensive data set on forest structure and composition, and the ability to statistically analyze and map these data in ways that were infeasible when Braun was writing.

Data for the present map of forest regions are derived from more than 100,000 Forest Inventory and Analysis (FIA) plots on both private and public lands in the eastern United States, monitored and administered by the US Forest Service. Summary data aggregated to the county level are available to the public. An examination of these county-level data for the eastern United States reveals the extent to which present-day forests have been modified (Miles 2001): The number of FIA sites is sparser in the agriculturally productive Midwest, and a high percentage of young, managed forest stands occur in the southern coastal plain. Iverson and Prasad (1998) used these data to create a county-level atlas for individual tree species of the eastern United States, and later created a finer-resolution gridded database, by averaging species data for all FIA plots occurring within 20 × 20 kilometer grid cells (Prasad and Iverson 2003).

For this study, importance value data were obtained for 7745 grid cells east of 100 degrees west (figure 2; Prasad and Iver-

son 2003). Importance values equally weight measures of relative density and relative dominance of both overstory and understory trees within a sample. Relative density represents the percentage of all individual stems comprised by a particular species, whereas relative dominance represents the percentage of the total basal area of all individuals comprised by that species; both density and dominance therefore provide different measures of how important a particular species is within a sample (abundance and size). Although importance values should sum to 100 for each grid cell, in some instances this was not the case, because of inconsistencies in how different divisions of FIA report species values (Iverson and Prasad 1998). For example, inspection of a grid cell whose importance values summed to 155 revealed that entries for "eastern cottonwood" (*Populus deltoides*) and "cottonwood and poplar species" were both 55; the double counting resulted in the sum of 155 for that cell. Such obvious discrepancies were manually corrected. The genus *Carya* (hickory) was more problematic. About 35 percent of the grid cells had a nonzero importance value for the undifferentiated "hickory species" taxon. For about 35 percent of these, this value represented the sum of the eight individual hickory species; for the remainder, it was unclear how the figure was derived, but double counting was suspected, since the sum of importance values was often well over 100. I retained all importance values for individual hickory species, but deleted the importance value for the undifferentiated "hickory species." Once all ad-

justments were made to the data set, importance values for any grid cell that still did not sum to 100 were relativized so that they did sum to 100. The total number of taxa across all cells was 186.

Grid cells were then subjected to a cluster analysis (PC-ORD version 4; McCune and Mefford 1999), which joins cells into hierarchical groups based on similarities in the importance values of their constituent species. The clustering method selected was flexible beta (ß = –0.25) using the Sørensen distance measure, which is generally recommended for community analysis (McCune and Grace 2002). Initial results showed fairly homogeneous groups (clusters) in the eastern United States, but a great deal of heterogeneity was revealed toward the western edge of the forest formation; many groups were composed of only a few cells, giving an overall salt-and-pepper appearance. A comparison with Bailey's (1995) map of ecoregions, depicting areas of similar climate with characteristic ecosystems, revealed that the boundary between his forest and nonforest provinces (figure 2) corresponded well with the western edge of the homogeneous cell groupings. The 6531 cells that fell within Bailey's forested provinces were used to run a final cluster analysis, and the results of the classification procedure were used to create a new forest regions map (figure 3). An initial inspection reveals both similarities and differences between the new forest regions (clusters) and Braun's map (figure 1).
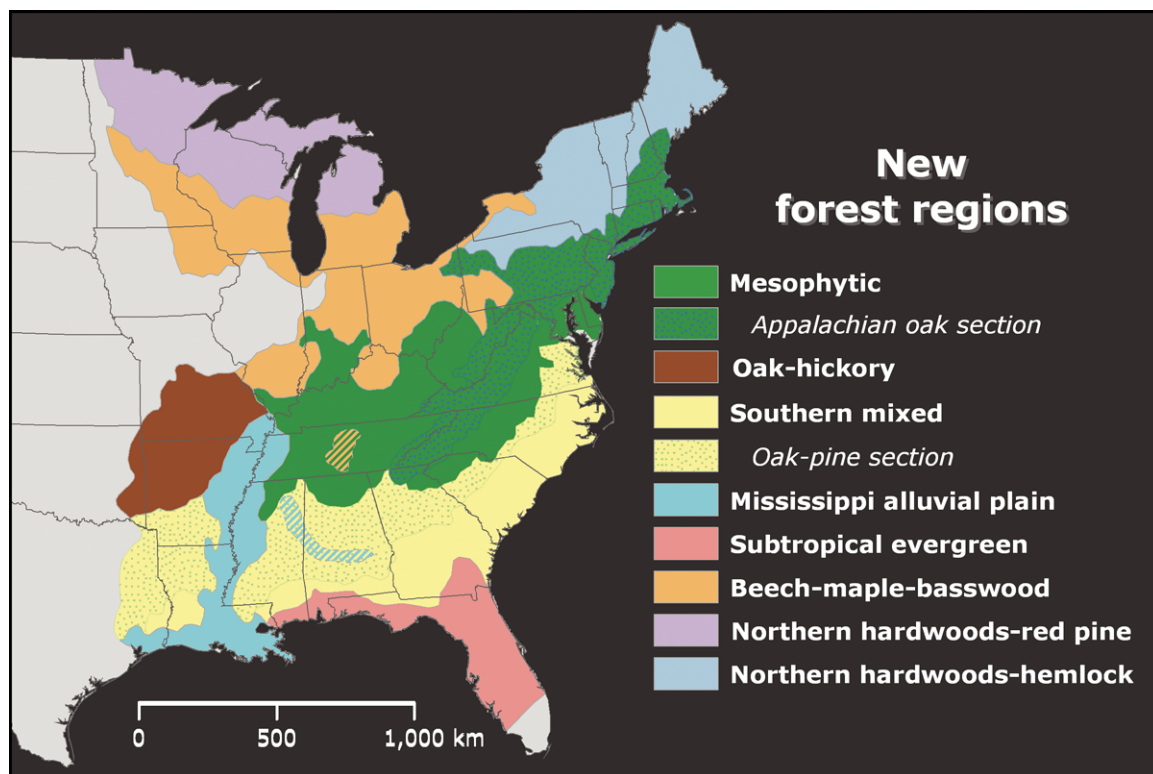

Figure 3. Regions derived from contemporary forest data. The cross-hatching in the Nashville Basin and the black belt region indicates inclusions within the larger forest regions—areas with affinities to the noncontiguous region with the same color as the cross-hatching.

Since the clustering procedure is hierarchical, with new groups formed by combining existing groups at each iteration, the final number of groups to retain can be a somewhat subjective decision. The goal is for groups to be homogeneous, contiguous regions that can be explained ecologically. Indicator species analysis (Dufrêne and Legendre 1997) provides an objective approach to determining the number of clusters to retain. At each level in the clustering hierarchy (four groups, three groups, etc.), an indicator value can be computed for each species within each group. The indicator value considers both *exclusiveness,* the degree to which a species is found only within one particular group, and *fidelity,* the percentage of sites (cells) that the species occupies within that group. A good indicator species is found predominately in a single group and is present in the majority of cells within that group. Using PC-ORD version 4 (McCune and Mefford 1999), I computed indicator values for each species by multiplying the species' mean importance value in a particular group (relative to its importance in all groups) by its relative frequency within that group. Thus, to be a good indicator species for a particular group, both importance and frequency must be high. A species' highest indicator value across all groups was retained as its overall indicator value. The statistical significance of this value was evaluated by performing a Monte Carlo simulation, randomly reassigning grid cells to groups 1000 times. A species' indicator value was considered significant when it exceeded the indicator value from the randomized data set ($p \leq 0.01$).

If natural groups are subdivided, indicator values of characteristic species will decrease; similarly, if natural groups are joined, internal heterogeneity within the new groups reduces indicator values (McCune and Grace 2002). Indicator values peak at an intermediate level of clustering, and the clustering level of this peak varies by species. Dufrêne and Legendre (1997) recommended using the sum of species-significant indicator values for each clustering level as a criterion for deciding when to stop the clustering procedure; the number of groups that yields the maximum sum represents the ideal number of groups for that data set. Figure 4 reveals that the sum of species-significant indicator values reaches its maximum with eight groups. Figure 4 also shows the sum of indicator value differences for each species at each step in the clustering hierarchy (from two groups to three groups, from three groups to four groups, etc.). From two to eight groups, high positive sums are observed, and the sum of all differences is positive. This suggests greater distinctiveness with the increasing number of groups, as indicator values for individual species are higher. (The exception is the step from four groups to five groups, when a "Midwest plus Mississippi alluvial plain" forest region separates from the previous four groups—northern, central, southern, and subtropical forest regions.) With more than eight groups, the sum of species-
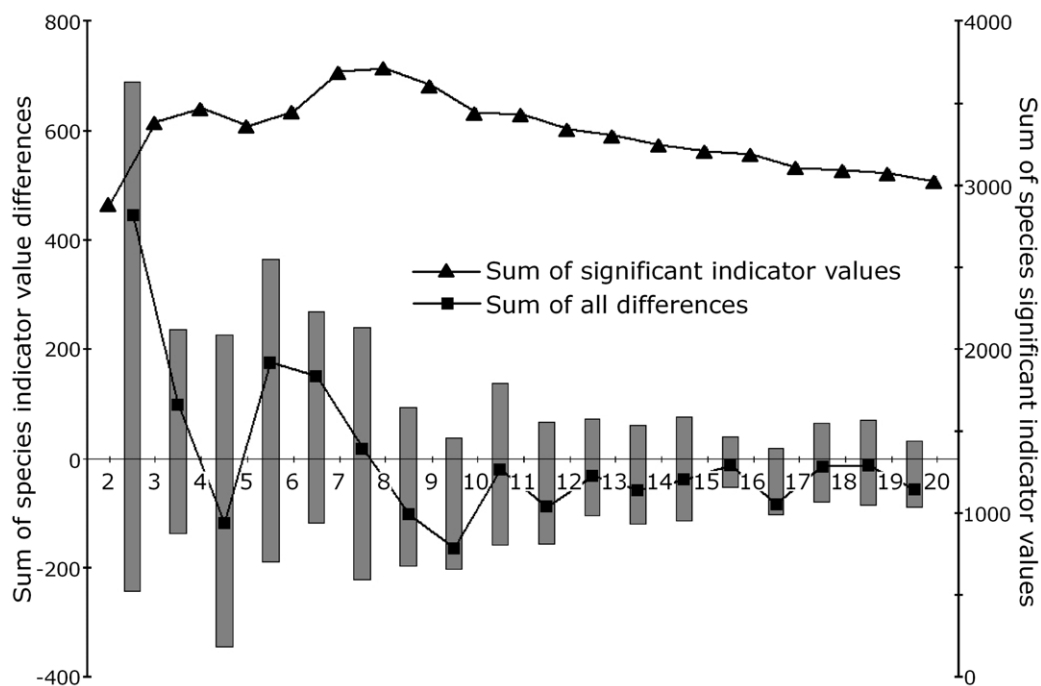
Figure 4. Sum of species indicator values used to determine the number of groups to retain in the clustering procedure. The number of groups is indicated along the x-axis, and triangles represent the sum of all species-significant (p ≤ 0.01) indicator values for that number of groups; the maximum sum occurs with eight groups. Bars represent the sum of positive differences and negative differences in indicator values between successive clustering levels; the squares represent the sum of all differences, which are always negative beyond eight groups.
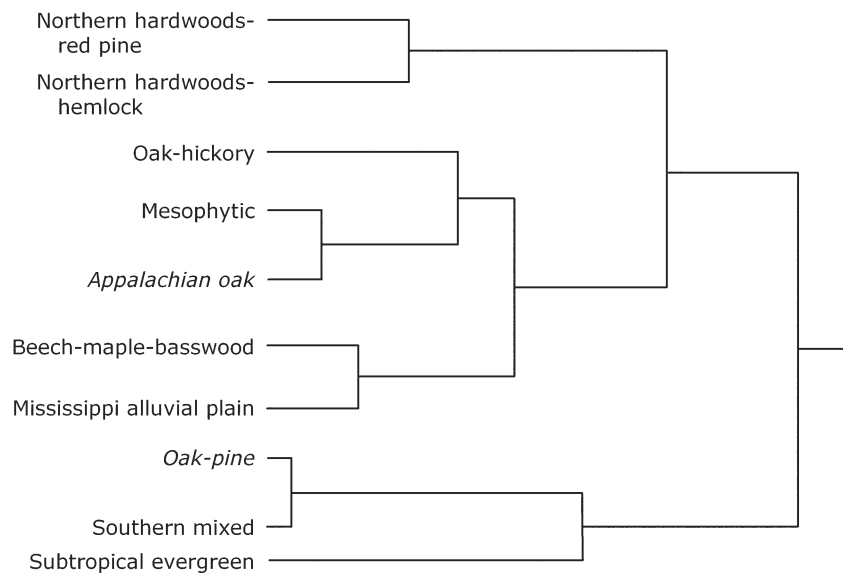
Figure 5. Dendrogram representing the flexible beta classification, showing the hierarchical relationship among eight forest regions and two forest sections (Appalachian oak, oak–pine).

significant indicator values continuously decreases, and the sum of indicator value differences is always negative.

Based on the results of the indicator species analysis, eight internally homogeneous forest regions are defined in the new map (figure 3). (For the sake of continuity, I elected to maintain Braun's naming conventions when possible.) Figure 3 also presents two sections (to borrow Braun's term for subdividing regions): the Appalachian oak section occurs within the mesophytic forest region, and the oak–pine section occurs within the southern mixed forest region. These sections represent the 9th and 10th clusters of the classification procedures, but as discussed above, they did not meet the statistical criterion to be designated as one of the eight forest regions. They are, however, long recognized by biogeographers, ecologists, and foresters, and considered by Braun to be distinctive forest regions on her map. No more than 10 clusters are identified in figure 3, because the resulting forest sections become noncontiguous. With 11 groups, for example, the northern hardwoods–hemlock forest region splits, with the Adirondack Mountains and northern New England separating from the rest of New York and northern Pennsylvania. (Braun recognized these sections within the northern Appalachian Highlands, but chose to group them in a single forest region that also encompassed a Great Lakes division [hemlock–white pine–northern hardwoods; figure 1].)

Figure 5 presents a dendrogram of the clustering procedure, showing the hierarchical relationship between the eight forest regions (and two sections). Table 1 lists significant indicator values for the eight forest regions. Only species with an indicator value of at least 35 percent are included in the table, which supposes that a characteristic species has a relative

frequency of at least 70 percent in one of the forest regions, and that its relative importance value in that region reaches at least 50 percent (Dufrêne and Legendre 1997). Table 2 is a confusion matrix (a cross-tabulation of actual versus predicted values in a classification procedure) demonstrating the homogeneity of the newly defined forest regions. For each forest region identified in figure 3, the percentage of cells within its boundaries belonging to that group is listed, as well as the percentage of its cells identified as belonging to other groups in the clustering procedure. The beech–maple–basswood region is most heterogeneous, with 26 percent of the cells within its borders classified as belonging to another forest region. Overall, however, the regions display a high level of internal homogeneity.

Overview and comparison with Braun's forest regions

Mesophytic forest region. This new forest region largely corresponds with three of Braun's regions: the mixed mesophytic, western mesophytic, and oak–chestnut. Seventy-three percent of cells within this region are circumscribed by the three Braun regions; it also includes part of the Atlantic slope section of her oak–pine forest region. According to Braun, the mixed mesophytic forest region, occurring in the unglaciated Appalachian plateaus, not only was centrally located geographically within the eastern deciduous formation but also represented the direct descendent of the ancient Tertiary forest, and thus from it all of the other forest regions arose. It is the most diverse forest region compositionally, with a large number of canopy dominants. Braun considered the western mesophytic forest region a transition zone to the drier oak–hickory forest region; overall there are fewer dominants in the western mesophytic region, with oaks and hickories increasing in predominance westward. As a result of the chestnut blight introduced into the United States in 1904, chestnut (*Castanea dentata*) trees were largely gone when Braun characterized her oak–chestnut forest region. She maintained the name, however, since she was unsure how succession would proceed within this forest region.

In the new analysis, the region is referred to simply as "mesophytic forest," since I noted no distinction between Braun's mixed mesophytic, western mesophytic, and oak–chestnut regions. As discussed previously, figure 3 does depict an Appalachian oak section within the mesophytic region, which is broadly coincident with Braun's oak–chestnut forest region. (Since many of the dominant species within this region are oaks [northern red oak, *Quercus rubra*; white oak, *Quercus alba*; black oak, *Quercus velutina*; scarlet oak, *Quercus coccinea*; chestnut oak, *Quercus prinus*], I have

Table 1. Indicator values, by forest region, for species with significant indicator values (≥ 35 percent).

Species	SE	Forest region						
		SM	MAP	B–M–B	O–H	M	NH–H	NH–RP
Slash pine (*Pinus elliottii*)	**81**	4	0	0	0	0	0	0
Live oak (*Quercus virginiana*)	**64**	0	0	0	0	0	0	0
Laurel oak (*Quercus laurifolia*)	**61**	12	1	0	0	0	0	0
Longleaf pine (*Pinus palustris*)	**51**	9	0	0	0	0	0	0
Pond cypress (*Taxodium distichum* var. *nutans*)	**50**	1	0	0	0	0	0	0
Sweetbay (*Magnolia virginiana*)	**43**	13	1	0	0	0	0	0
Redbay (*Persea borbonia*)	**42**	7	0	0	0	0	0	0
Swamp tupelo (*Nyssa sylvatica* var. *biflora*)	**38**	17	0	0	0	0	0	0
Loblolly pine (*Pinus taeda*)	5	**65**	7	0	1	1	0	0
Sweetgum (*Liquidambar styraciflua*)	4	**41**	25	0	2	4	0	0
Water oak (*Quercus nigra*)	17	**39**	16	0	0	0	0	0
Sugarberry (*Celtis laevigata*)	0	0	**45**	0	1	0	0	0
Green ash (*Fraxinus pennsylvanica*)	0	1	**42**	9	2	1	1	4
American elm (*Ulmus americana*)	0	0	13	**35**	6	3	8	7
Black hickory (*Carya texana*)	0	0	0	0	**85**	0	0	0
Post oak (*Quercus stellata*)	0	8	4	0	**72**	2	0	0
Blackjack oak (*Quercus marilandica*)	0	3	0	0	**65**	0	0	0
Black oak (*Quercus velutina*)	0	1	1	7	**56**	13	0	0
White oak (*Quercus alba*)	0	7	2	12	**37**	19	1	1
Eastern redcedar (*Juniperus virginiana*)	0	2	2	5	**35**	7	0	0
Chestnut oak (*Quercus prinus*)	0	1	0	0	0	**51**	1	0
Yellow poplar (*Liriodendron tulipifera*)	1	17	1	1	0	**45**	0	0
Virginia pine (*Pinus virginiana*)	0	2	0	0	0	**39**	0	0
Yellow birch (*Betula alleghaniensis*)	0	0	0	0	0	1	**55**	12
Eastern hemlock (*Tsuga canadensis*)	0	0	0	0	0	5	**51**	4
American beech (*Fagus grandifolia*)	0	2	1	1	0	13	**50**	1
Sugar maple (*Acer saccharum*)	0	0	0	7	1	9	**48**	15
Striped maple (*Acer pensylvanicum*)	0	0	0	0	0	2	**45**	0
Red spruce (*Picea rubens*)	0	0	0	0	0	0	**38**	0
Quaking aspen (*Populus tremuloides*)	0	0	0	3	0	0	9	**77**
Black spruce (*Picea mariana*)	0	0	0	0	0	0	2	**63**
Balsam poplar (*Populus balsamifera*)	0	0	0	0	0	0	1	**61**
Paper birch (*Betula papyrifera*)	0	0	0	1	0	0	16	**59**
Tamarack (*Larix laricina*)	0	0	0	0	0	0	3	**58**
Jack pine (*Pinus banksiana*)	0	0	0	1	0	0	0	**54**
Black ash (*Fraxinus nigra*)	0	0	1	2	0	0	6	**52**
Red pine (*Pinus resinosa*)	0	0	0	2	0	0	3	**50**
Northern white cedar (*Thuja occidentalis*)	0	0	0	0	0	0	11	**46**
White spruce (*Picea glauca*)	0	0	0	0	0	0	9	**45**
Bigtooth aspen (*Populus grandidentata*)	0	0	0	4	0	1	11	**43**
Balsam fir (*Abies balsamea*)	0	0	0	0	0	0	24	**41**

B–M–B, beech–maple–basswood; M, mesophytic; MAP, Mississippi alluvial plain; NH–H, northern hardwoods–hemlock; NH–RP, northern hardwoods–red pine; O–H, oak–hickory; SE, subtropical evergreen; SM, southern mixed.

Note: Figures in boldface represent the highest indicator value for that species across all forest regions.

used the designation "Appalachian oak" for this section.) The mesophytic is the largest of the new forest regions, and with 162 species it is also the most diverse. As with Braun's mixed mesophytic forest, no species assumes canopy dominance across the region. Of the grid cells containing FIA plots, red maple and white oak occur in 87 percent and 86 percent of cells, respectively; red maple has the highest average importance value (10.9 overall, 16.5 in the Appalachian oak section), with white oak second (5.3 overall).

Oak–hickory forest region. Braun recognized a northern (glaciated) and southern (unglaciated) division within her oak–hickory forest region. Most grid cells in the northern division, which today is dominated by crop production, were deleted from the new map, since they occurred within a non-forested province (figure 2). Thus, the oak–hickory region of the new forest map is largely restricted to the interior highlands of Arkansas and Missouri. Ninety-seven percent of its cells lie within Braun's oak–hickory forest region. Braun

Table 2. Confusion matrix showing results of the classification procedure.

	SE	SM	MAP	B–M–B	O–H	M	NH–H	NH–RP
Subtropical evergreen	**80.4**	16.7	2.9	0.0	0.0	0.0	0.0	0.0
Southern mixed	1.4	**87.3**	7.1	0.2	1.2	2.7	0.0	0.0
Mississippi alluvial plain	0.5	6.2	**81.2**	3.0	3.0	6.1	0.0	0.0
Beech–maple–basswood	0.0	0.0	4.6	**74.1**	0.2	8.7	10.5	2.0
Oak–hickory	0.0	0.3	4.1	5.9	**87.5**	2.1	0.0	0.0
Mesophytic	0.0	2.4	1.3	4.9	0.5	**88.2**	2.8	0.0
Northern hardwoods–hemlock	0.0	0.0	0.0	2.5	0.0	3.3	**90.1**	4.1
Northern hardwoods–red pine	0.0	0.0	0.9	2.2	0.0	0.2	17.7	**78.9**

B–M–B, beech–maple–basswood; M, mesophytic; MAP, Mississippi alluvial plain; NH–H, northern hardwoods–hemlock; NH–RP, northern hardwoods–red pine; O–H, oak–hickory; SE, subtropical evergreen; SM, southern mixed.

Note: Each row represents a forest region depicted in figure 3; values represent the percentage of grid cells within that region that were classified into each forest region, indicated by the column headings. Boldface indicates the percentage of cells within a forest region that were correctly predicted.

characterized this drier, westernmost section of the deciduous forest as being dominated by oak and hickory species, and this characterization still holds with the new forest region. Post oak (*Quercus stellata*), black oak, black hickory (*Carya texana*), white oak, and mockernut hickory (*Carya tomentosa*) each occurs in more than 90 percent of grid cells containing FIA plots, with average importance values above 10.0 for post oak, white oak, and black oak.

Southern forest regions. Braun recognized two forest regions in the Southeast: the oak–pine and the southeastern evergreen forest regions; two regions are delineated on the new map as well. (I have also included a subtropical evergreen forest region, which Braun did not include because it was not part of the deciduous forest formation.) Differences between the maps do exist, however, as Braun's oak–pine region has been delineated as a section within the southern mixed region on the new map. (I have elected to use "southern mixed" instead of Braun's "southern evergreen" to acknowledge the numerous deciduous trees that characterize this forest region, and to distinguish it more clearly from the subtropical evergreen forest.) Also, the Mississippi alluvial plain section within Braun's southeastern evergreen region is recognized as a separate region on the new map. Overall species characterizations of these forest regions are similar between Braun and the new maps, and in the eastern United States there is close agreement of their boundaries.

Braun characterized the oak–pine and southeastern evergreen forest regions as transitional, between the deciduous forest to the north and the subtropical broadleaved evergreen forest to the south. She considered the oak–pine forest region to be essentially an extension of the oak–hickory forest region, although qualitatively different because of the presence of more pines, especially loblolly (*Pinus taeda*). Braun believed, however (perhaps reflecting her Clementsian influence), that the pines were largely temporary features, to be replaced by deciduous species as succession proceeded. Her southeastern evergreen forest region was confined to the coastal plain and was dominated by evergreens, especially longleaf pine (*Pinus palustris*), though deciduous communities did occur in a

secondary role. Braun attributed the distinctiveness of this forest region to the well-drained sandy soils of the coastal plain and to the subsequent role of fire.

In the new map, some differentiation is observed within the southern mixed forest region, though this differentiation is not sufficiently pronounced to warrant the designation of two separate regions. A marked decrease in hickory species occurs southward, and longleaf pine is more common on the coastal plain. Other notable compositional changes include an increase in swamp tupelo (*Nyssa sylvatica* var. *biflora*), laurel oak (*Quercus laurifolia*), sweetbay (*Magnolia virginiana*), redbay (*Persea borbonia*), and slash pine (*Pinus elliottii*). (Slash pine becomes the dominant species in the subtropical evergreen forest, with the highest average importance value [31.1] of any species in any forest region.) However, throughout the inclusive southern mixed forest region, loblolly pine is the most prominent species (with an average importance value of 25.4); loblolly pine, sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), southern red oak (*Quercus falcata*), and red maple occur in more than 85 percent of the grid cells in the region containing FIA plots. The boundaries of Braun's southeastern evergreen and oak–pine forest regions are similar to those of the southern mixed region and oak–pine section of the new map in the east, but diverge along the Gulf coastal plain. Also, Braun's southeastern evergreen forest extends into northern Florida, whereas this area is considered part of a subtropical evergreen forest region in the new map.

The last southern forest region in the new classification is the Mississippi alluvial plain. Braun recognized the "bottomland forests" of this area as a section within her southeastern evergreen forest region. Although forest density is extremely low in this area, its compositional distinctiveness warranted its designation as a separate forest region in the new map. Dominant species include sweetgum, green ash (*Fraxinus pennsylvanica*), sugarberry (*Celtis laevigata*), American elm (*Ulmus americana*), bald cypress (*Taxodium distichum*), and loblolly pine (with an average importance value of 6.3, compared with 25.4 in the southern mixed forest region, which borders it to the east and west). The crescent-shaped

"black belt" region of Alabama and Mississippi, known for its rich, dark soil, could also be considered part of this forest region; however, owing to its smaller size and the fact that it is not contiguous with the Mississippi alluvial plain, it was instead treated as an inclusion within the southern mixed forest region.

Beech–maple–basswood forest region. Braun recognized two related forest regions in the Midwest: beech–maple and maple–basswood. Her beech–maple forest region was mostly restricted to the glaciated parts of Ohio, Indiana, Michigan, and western New York; much of this area is now converted to cropland. Maple–basswood was the smallest forest region that Braun defined, primarily restricted to the unglaciated Driftless Area of Wisconsin. She acknowledged that the maple–basswood forest could be considered a variant of the beech–maple forest region, but elected to treat it separately because of its isolation and different glacial history. In the current analysis, these two regions were not sufficiently distinctive, so a single beech–maple–basswood forest region was designated. (The agricultural landscape of the Midwest was the most heterogeneous of all regions, interspersed with grid cells with affinities to neighboring forest regions; see table 2.) In the Midwest, the beech–maple–basswood forest region extends beyond the glacial boundary into northern Kentucky; the Nashville Basin in central Tennessee is also compositionally similar to this forest region, but because of its isolation and limited extent, it was treated as an inclusion within the mesophytic forest region.

Compositionally, American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and American basswood (*Tilia americana*) have long been distinctive components of the regional forest, and I have chosen to maintain these species names to designate the region because of this long-term association. However, these species are not the most dominant within this forest region, and in fact each attains higher importance values in other forest regions. Dominants in the beech–maple–basswood forest region include American elm, black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), northern red oak, and white oak.

Northern hardwoods–conifer forest regions. Braun considered her hemlock–white pine–northern hardwoods forest region to be transitional between the deciduous forest to the south and the boreal forest to the north. Although she observed compositional differences within it, she elected to delineate a single forest region. For example, she noted that the Great Lakes–St. Lawrence division was characterized by red and eastern white pines (*Pinus resinosa* and *Pinus strobus*, respectively), whereas eastern hemlock (*Tsuga canadensis*) and red spruce (*Picea rubens*) characterized the northern Appalachian highland division. Despite these differences, she may have elected to delineate a single forest region because of its transitional nature with the deciduous forest formation, her primary focus. In the present analysis, compositional differences warranted the delineation of two separate forest

regions; 94 percent of cells within each of the two new regions fall within Braun's hemlock–white pine–northern hardwoods forest region.

The northern hardwoods–red pine forest region, with 77 species, has the lowest diversity of the forest regions. Braun noted that her Great Lakes division contained mostly secondary forests, thus giving little indication of presettlement forest types. This observation is reflected in the current composition: The successional quaking aspen (*Populus tremuloides*) is the most dominant species, occurring in 100 percent of grid cells containing FIA plots, with an average importance value of 20.0. Other principal species include red maple, balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*). Sugar maple is much more dominant in the northern hardwoods–hemlock forest region, occurring in 97 percent of cells containing FIA plots, with an average importance value of 14.0. Red maple is second in terms of both frequency of occurrence and importance; other key species include American beech and white ash.

Differences between the maps

The boundaries of forest regions in the two maps diverge somewhat. Some of these differences can be attributed to splitting or lumping decisions. For example, as previously discussed, Braun's hemlock–white pine–northern hardwoods region is split into two northern hardwoods–conifer regions in the new map. Her maple–basswood and beech–maple forest regions, which she considered similar, have been combined into a single region in the new map.

A more notable boundary shift is observable between Braun's southeastern evergreen and oak–pine forest regions compared with the corresponding boundary between the southern mixed forest region and the oak–pine section of the new map. Along the Gulf Coast, Braun shows this boundary beginning in central Mississippi and Alabama, with the southeastern evergreen forest extending southward to the panhandle and parts of northern Florida. In the new map, this boundary occurs in southern Mississippi and Alabama, and the oak–pine section occupies a much broader area along the Gulf Coast.

Several lines of evidence support the new map's boundary placement. Much of the area in central Mississippi and Alabama that Braun classified as southeastern evergreen forest, dominated by longleaf pine, is now in production forestry with loblolly and shortleaf pine (*Pinus echinata*). The current boundary more closely coincides with present-day forest cover types (Eyre 1980). In addition, the boundary on the new map coincides closely with the oak–hickory–pine and southern mixed forest vegetation types in Küchler's (1964) map of "natural" vegetation for this area. The reason for the boundary discrepancy with Braun's map is unclear, though it has been noted that the southern coastal plain was not well represented in her work (Monk et al. 1989).

The other notable difference between Braun's map and the new map centers around her mixed mesophytic forest region. Braun considered this region to be the "core" of the eastern

deciduous forest formation, with very high species diversity and numerous canopy dominants. Throughout her western mesophytic forest region, which borders the mixed mesophytic forest to the west, there was a gradual transition as the forest became less luxuriant, with a greater tendency toward canopy dominance by fewer species. To the east, oaks and yellow poplar dominated the steeper slopes of her oak–chestnut region. In the new classification, Braun's mixed mesophytic, western mesophytic, and oak–chestnut regions and the Atlantic slope section of her oak–pine forest region were not differentiated. Many of the dominant species of Braun's mixed mesophytic forest region still are dominant in the new mesophytic forest region, and a number of her indicator species (white basswood, *Tilia heterophylla;* yellow buckeye, *Aesculus octandra;* chestnut oak; chinkapin oak, *Quercus muehlenbergii*) still demonstrate the same affinities for either her mixed mesophytic forest or her western mesophytic forest region.

Subsequent studies that employed multivariate statistical analyses using some of Braun's (1950) original stand data (Monk et al. 1989, Delcourt and Delcourt 2000) show a great deal of overlap between Braun's mixed mesophytic, western mesophytic, and oak–chestnut forest regions. Although she designated them as separate regions, Braun did note the intermingling of community types between them. It should be noted that although she considered the herbaceous understory important in distinguishing the regions, the present classification (as well as those using Braun's published stand data) does not consider it. (However, several studies have documented dramatic changes in the herbaceous understory in second-growth forests, compared with old-growth forests; see Duffy and Meier 1992, Matlack 1994, Bellemare et al. 2002, Flinn and Marks 2004.) It is likely, though, that the lack of distinctiveness revealed by the data reflects changes in the abundance of woody species in secondary forests compared with the old-growth forests on which Braun focused.

Historic land-use practices have dramatically affected the composition of secondary forests in the eastern United States (Whitney 1990, Orwig and Abrams 1994, Cowell 1998, Radeloff et al. 1999). Before European settlement, forest species assemblages demonstrated patterns consistent with gradients of climate and physiography (Foster et al. 1998). Although the distributions of individual species have not changed markedly, shifts in species abundance have resulted; in many regions, clearing and abandonment have favored well-dispersed early successional species (such as red maple) and a concomitant decline in longer-lived shade-tolerant species. Broadscale similarities in land use have tended to mask regional environmental controls (Foster 1992, Russell et al. 1993). Homogenization of species composition is noted in the new forest regions, especially in the prevalence of red maple. Abrams (1998) noted the dramatic increase in importance of red maple in eastern forests since the presettlement period, which he attributed to its ability to adapt to environmental and land-use changes. Since the species has traits of both early successional and climax species, it has increased in

abundance after agricultural abandonment and where periodic fires have been suppressed. Red maple occurs in more than 85 percent of the grid cells containing FIA plots in mesophytic, southern mixed, and both northern hardwoods–conifer forest regions. In terms of its average importance value across the grid cells, it is ranked first in the mesophytic forest region and in the top 10 of all regions except the oak–hickory forest.

Conclusions

In this revisiting of the mapping of eastern US forest regions, clear differences emerge between Braun's and the present map. The degree to which the geography of Braun's forest regions is largely maintained on the new map is notable, however (though changes in species abundances within the forest regions have most likely occurred since Braun described them). Likewise, the locations of at least some of the *boundaries* between forest regions are consistent across the two maps, especially if the two forest sections (Appalachian oak, oak–pine) are considered. The similarities between the two maps are noteworthy, considering the differences in the methodologies behind their creation, as well as the changes in forest conditions that have resulted from intensive land-use change, fire suppression, introduction of exotic species, and changes in atmospheric chemistry since Braun's work.

Braun relied heavily on her own field sampling, whereas the current map is based on an extensive network of FIA plots distributed across the eastern United States. Since Braun could not achieve the same level of coverage with her own sampling, one might expect that her map would be colored by her Clementsian ecological bias. It has been noted that she extrapolated her forest regions so that their boundaries often coincided with physiographic boundaries (Delcourt and Delcourt 2000). In contrast, forest regions on the new map were defined from a cluster analysis based solely on species data. Another significant difference between the two maps is that Braun aimed to describe "original" forests, focusing on old-growth stands, whereas the present map was based on contemporary forest composition and structure. The correspondence between the maps despite these differences speaks to Braun's perceptiveness and abilities as a forest ecologist.

This correspondence across methodological differences and marked forest changes raises the question of what makes these forest regions distinctive. Especially at this coarse spatial scale, climate no doubt has a strong influence on the distribution of individual species and communities, as Braun noted. Although there is a great deal of overlap, plotting sample locations from the new forest regions along moisture and energy axes shows a strong temperature signal, with the subtropical evergreen forest and the northern hardwoods–conifer forest regions serving as endpoints; seasonal moisture differences further separate the forest regions (e.g., distinguishing the drier northern hardwoods–red pine from the more humid northern hardwoods–hemlock forest). An inspection of the present map of forest regions also reveals associations between some of the regions and other abiotic

factors, including soil orders and physiographic regions. For instance, 75 percent of cells within the Mississippi alluvial plain region have soils classified as alfisols or vertisols, though neighboring regions are predominately ultisols (NRCS 1998). The majority of cells (66 percent) within the beech–maple–basswood region are also classified as alfisols (NRCS 1998), and its southern boundary mirrors the glacial boundary (figure 2). The oak–hickory region corresponds almost perfectly with Fenneman's (1938) interior highland physiographic division.

Disturbance, especially fire, has probably been critical in establishing the boundaries of some forest regions (e.g., southern mixed forest). Migration responses to past climatic changes might also play a role in the distinctiveness of the forest regions, as Braun suggested. During the glacial maximum 18,000 years ago, species found refuge in different areas of what is now the eastern United States, and as the glaciers retreated, species migrated along different routes. For example, today American beech and sugar maple are common associates, especially prominent in the forests of the Great Lakes region and extending into New England. However, after the glacial maximum 18,000 years ago, palynological evidence suggests that beech was found primarily in the southern Appalachians, and by the start of the Holocene 10,000 years ago had spread to much of the southern coastal plain, north of the Florida peninsula. It then migrated rapidly up the eastern seaboard into New England and the Great Lakes region. In contrast, maple appears west of the Appalachians following the glacial retreat, migrating to its current range from the West (Williams et al. 2004). Although the nature of the forest response to climatic change appears different from what Braun hypothesized, these two taxa illustrate the individualistic responses of forest species to climate change since the last glacial maximum, and demonstrate that today's forest regions represent recent associations. Differential species responses thus may play a role in the distinctiveness of forest regions.

Regardless of the precise mechanisms responsible for creating these forest regions, it is evident that at least some of their boundaries appear to have remained fairly consistent in the face of dramatic environmental change since the settlement period. Although some compositional changes have occurred, many similarities exist between today's forest regions and Braun's, despite major shifts in land use and disturbance regimes. Whether the similarities can be maintained in the face of continuing environmental change will be an issue for future research.

Acknowledgments

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Williams JW, Shuman BN, Webb T, Bartlein PJ, Leduc PL. 2004. Late Quaternary vegetation dynamics in North America: Scaling fr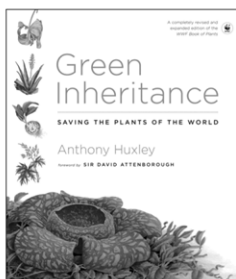om taxa to biomes. Ecological Monographs 74: 309–334.