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Change in oak abundance in the eastern United States from 1980 to 2008

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ABSTRACT

Although oaks (*Quercus* spp.) have historically dominated much of the forest land in eastern North America, a great deal of fragmentary and sometimes anecdotal evidence suggests that they have been yielding dominance in recent decades to other, typically more shade-tolerant species. Using FIA data, our work formally quantifies the change in oak abundance in the eastern U.S. during the period of 1980–2008. The results indicate that most areas in the eastern U.S. experienced some decline in oak abundance, but the decrease was not universal either geographically or among species. Declines were especially marked in the Central Hardwood Region, which lost oak abundance on 81% its forested area as measured by importance value (IV). Areas with a high oak abundance were more likely to see a reduction in abundance. Among all 25 species analyzed, eight species decreased significantly in IV while two increased. Both the top two most prevalent white oak species (white oak (*Quercus alba*) and post oak (*Quercus stellata*)) and red oak species (northern red oak (*Quercus rubra*) and black oak (*Quercus velutina*)) had significant decreases in density and IV. Water oak (*Quercus nigra*) is one of the red oak species that had a near universal increase of its abundance throughout its native range (83% of area). This study provided a comprehensive quantification of the dynamic of oak species in a regional-wide geographic context, which will provoke forest researchers and managers to revisit the oak decline problem by using knowledge from other regions and other species.

1. Introduction

Oak (*Quercus*) is the largest tree genus in number of species in the United States, and oak species are native to every state except Idaho, Alaska, and Hawaii. Oak is particularly abundant in the eastern U.S., where its species are predominant or associated components of 68 of 90 forest cover types (Eyre, 1980). Nearly one-fourth of all growing stock on timberland in the eastern forests is in oak trees (Smith et al., 2003). Oaks play an unusually important role in the ecosystem by providing food and habitat for many species of animals, they are economically important because of their useful and sometimes quite valuable timber, and they are treasured for cultural and historical reasons. Unfortunately, many regional studies have pointed to significant declines in oak abundance (Johnson, 1976; Abrams and Nowacki, 1992; Lorimer, 1993). The reasons for these declines are presumably related to exogenous and unprecedented factors such as new disturbance regimes, fire suppression, invasion of exotic species, climate change, and/or modern wildlife and forest management practices, but the precise causes are unclear and probably complex. Challenges to maintaining a strong oak component in forest stands have generated scores of research papers related to the topic. But oak dominance appears to be steadily eroding despite the existence (and, presumably the application) of a rather extensive body of research-based guidance for regenerating and managing oak stands (e.g., Hibbs and Bentley, 1983; Loftis and McGee, 1993; Steiner et al., 2008).

While a decline in oak abundance is reported to be occurring widely (Crow, 1988; Abrams, 2003; Moser et al., 2006), both geographically and among species, our knowledge of the phenomenon is based largely on localized evidence. McWilliams et al. (2002) provided a comprehensive summary of oak abundance across the region and discussed the potential for changes as suggested by mortality data. However, to our knowledge, only Moser et al. (2006) has addressed region-wide changes, and their study focused on basal area and regeneration abundance and proportion (Moser et al., 2006). Thus, although the phenomenon is almost a matter of conventional wisdom among experts, there lacks comprehensive assessment of its magnitude, extent, and scope. If a decline in oak

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abundance is occurring, how rapidly is it happening? Is it happening everywhere in the eastern U.S. where oaks are an important component of forests? And is it happening to all species of oak throughout all of their natural distributions? Nowacki and Abrams (2008) have cautioned that the time for restoring oak-dominant ecosystems may be running out, as systems may be approaching critical ecological thresholds and near-irreversible state shifts. A comprehensive and quantitative description of this phenomenon is pressingly needed in order to better understand the significance of problem and develop sound strategies with which to confront it. In this study, we used inventory data from the eastern U.S. to describe changes in oak abundance during the period of 1980–2008.

2. Materials and methods

Data from the USDA Forest Service Forest Inventory and Analysis (FIA) National Program were used in this study (USDA FS, 2008). The FIA database is a long-term record of information on the status and trends of America's forest resources based upon field samples distributed across the landscape with approximately one sample location every 2428 ha (6000 ac). All states were inventoried periodically, but at irregular and asynchronous intervals before 2000. Most states have been inventoried annually, but partially, since 2000. For this study, we used Forest Inventory Mapmaker 3.0 (Miles, 2008) to capture county-level information on the total number and whole stem volume of all live trees for all species in the eastern 37 states of the U.S., defined here as North Dakota south to Texas and all states to the eastward (Fig. 1). For most states we obtained data from two or more completed inventories, beginning with the first available measurement after 1980. The first inventory (T_1) for each state was a periodic survey conducted between 1980 and 1995 depending on the state. The second inventory (T_2) was defined as the latest available periodic survey or full-cycle, annual survey (all plots) as of June 2008. The interval between the two inventories ranged from 8 to 20 years with an average of 16.4 years. Because a full-cycle, annual survey takes 5 to 7 years to complete, the median year was used to calculate the interval. In total, we used data from all 2625 counties in 37 eastern states in the U.S.

Importance value (IV) was used to describe relative abundance of oak for each inventory. An ecological metric, IV is conventionally defined as the sum or average of relative measures of density, dominance, and frequency. In this study, we adapted the concept by defining IV as the mean of (1) relative density (total number of oaks/total number of all live trees $\times$ 100) of trees with a diameter of at least 2.54 cm (1.0 inch) and (2) relative volume or dominance (total growing stock volume of oak/total growing stock volume of all live trees $\times$ 100). To understand the general trend of current oak abundance, a contiguous surface was developed for all oaks, all white oak species (*Quercus* section *Quercus*), and all red oak species (*Quercus* section *Lobatae*). Oak abundance from the most recent inventory within each county was first assigned to the county centroid, and then extrapolated to form a continuous surface using the Ordinary Kriging (12 nearest point search radius, 1 km^2 resolution) method in ArcGIS (ESRI Inc., Redlands, CA). Non-forested areas (based on the 2001 National Land Cover Dataset, USGS, 2008) were removed from the surface to more accurately reflect the distributions.

Changes in oak density and volume during the study period were analyzed by oak section and genus, and statistical significance of these changes within each section and entire genus was tested using paired *t*-tests based on county level attributes. Changes in relative density, relative volume, and IV during the study period were analyzed by ecoregion in which oaks most commonly occur: Northern Hardwood Region, Central Hardwood Region, Southern Pine-Hardwood Region, and Forest-Prairie Transition Region (Bailey, 1997; Johnson et al., 2002) (Fig. 1). Because the intervals between T_1 and T_2 are different for each state, an annual change rate was calculated by using the overall difference between T_1 and T_2 divided by interval length to eliminate the variability introduced by different sampling intervals. Trend surfaces were then developed for annual changes in the above measures and non-forested areas were excluded. Percentages of areas within each ecoregion and across the eastern U.S. that experienced an increase or decrease in oak abundance were tabulated in ArcGIS.

To better reveal the specific changes that occurred during the two inventory periods, changes in oak abundance were further analyzed by species. For all 25 individual species analyzed (Table 3), grand means were calculated for each species, and a paired *t*-test analysis was applied to examine whether the changes in relative density, relative volume, and IV were statistically significant, using county-level measures to calculate the variations. Annual change in IV was further calculated by county for the four most prevalent white oak species and five red oak species. Prevalence was determined by tabulating the total number of counties in which a given species occurred. Annual IV change trend surface was then mapped within their respective natural distributions (Little, 1971, 1977) on forested areas.

3. Results

3.1. Spatial distribution of oak abundance

Among the four regions in the eastern U.S., the Central Hardwood Region has the highest oak abundance (Fig. 2a). The Central Hardwood Region hosted more than half of the total volume (1743/3248 million m^3) of all oak species in the eastern forest. Within the Central Hardwood Region, the Ozark Plateau (southern Missouri and northern Arkansas) has the highest oak abundance (>over 40% in IV), and portions of the Appalachians from Pennsylvania southward and the adjacent Cumberland Plateau have significant concentrations of oak (IV > 20%). Within the Southern Pine-Hardwood Region, oak is most dominant in northern Georgia and Alabama and, also, eastern Texas and adjacent parts of Louisiana and Arkansas. Oak is rather sparsely but widely presented across most of the Northern Hardwood Region, and the greatest concentrations occur along the southern edge of the region where it borders the Central Hardwoods. For the Forest-Prairie Transition Region, only limited area in the south (Oklahoma and Texas) and east (northern Missouri and Illinois) has notable oak abundance.

Geographic patterns of abundance differ between white and red oaks (Fig. 2b and c). Oaks in the white oak group have their greatest abundance in the central part of the eastern U.S., primarily in the southern and Appalachian portions of the Central Hardwood Region (Fig. 2b). White oaks are generally more abundant than red oaks throughout the Central Hardwood Region, except that both groups are highly prominent on the Ozark Plateau. In contrast, red oaks have relatively higher abundance than white oaks in both the north and the south, i.e., much of the Southern Pine Region and portions of the Northern Hardwood Region and adjacent areas in the Central Hardwood Region (Fig. 2c).

3.2. Changes in density and volume of oak

In general, oaks lost density but gained volume during the study period. Overall oak density decreased 13% between the two inventory periods but gained 18% in volume (Table 1). On average, species in the white oak group had a higher decrease in density (20.4 tree/ha or 22%) than species in the red oak group (4.1 tree/ha or

Fig. 1. The major ecoregion divisions where oaks commonly occur (Northern Hardwood Region, Central Hardwood Region, Southern Pine-Hardwood Region, and Forest-Prairie Transition Region; Bailey, 1997; Johnson et al., 2002) and their underlying physiographic provinces and sections in the eastern U.S.

4%), but a higher increase in volume (3.3 m^3/ha or 23%, 2.7 m^3/ha or 18%, respectively). Five white oak species and seven red oak species had significant decreases in density, and only two species, water oak and Shumard oak (both red oaks), had significant increases (Table s1). Three white oak species and eight red oak species had significant increases in volume, and only two species, blackjack oak and bluejack oak (both red oaks), had significant decreases.

Sixty percent of the eastern forest experienced a decrease in oak density between T_1 and T_2, and decreases were especially great in the Central Hardwood Region (Fig. 3a, Table s2). About 87% of the Central Hardwood Region experienced some decrease in oak density, with the sharpest decline occurring on the Ozark Plateau. The other areas with widespread decreases in oak density were the Cumberland Plateau in Kentucky and Tennessee and a majority of the central and southern Appalachians. Forests in the Forest-Prairie Transition Region also had a prevalent (79%) decline in oak density. On the other hand, the majority of the Northern Hardwood Region (67%) and some portions of the Southern Pine-Hardwood Region experienced an increase in oak density. Eastern Texas, southwestern Mississippi, and most of Georgia increased in oak density.

The majority of the eastern forest (>82%) exhibited an increase in oak volume (Fig. 3b). The percentage of forested area that increased in oak volume was highest in the Northern Hardwood Region (90%), and lowest in the Forest-Prairie Transition Region (56%). In the Central Hardwood Region, the Ozark Plateau, the Cumberland Plateau, the southern Appalachians, and southern New England all had large increases in oak volume (>0.5 m^3/ha/year), while the Driftless Section in southeastern Wisconsin and adjacent Minnesota had a prominent decrease in oak volume.

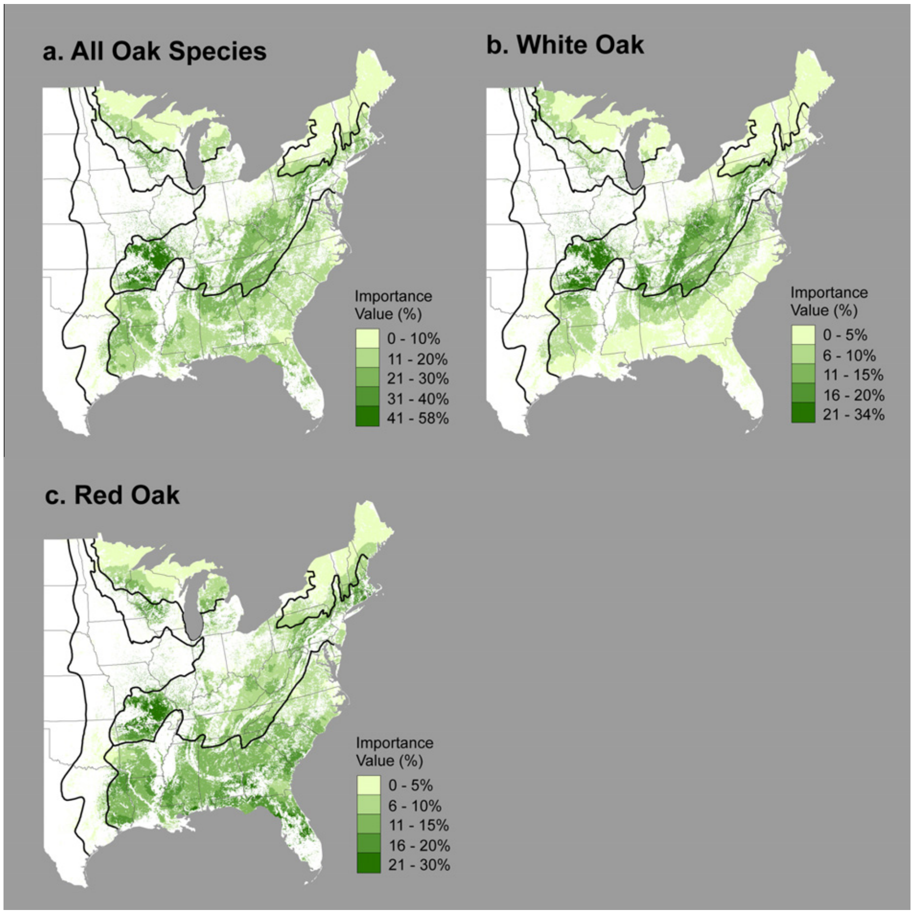

Fig. 2. Current abundance, as measured by importance value ((relative density + relative volume)/2), for (a) all oak species, (b) white oak species, and (c) red oak species in the eastern U.S. forested areas.

Table 1
Changes in oak density and volume by section and the entire genus between the first (T_1) and second (T_2) inventory during the last two decades; all changes between T_1 and T_2 are significant at $p < 0.001$.

Species group	Density (num/ha)		Volume (m^3/ha)	
	T_1	T_2	T_1	T_2
White oaks (section *Quercus*)	92.1	71.7	14.1	17.4
Red oaks (section *Lobatae*)	115.8	111.7	15.1	17.8
All oaks	196.5	170.6	27.7	32.7

3.3. Changes in relative density, volume, and importance value of oak

Decreases in oak relative density were significant in all regions except for the Northern Hardwood Region (Table 2). The decrease was the highest in the Forest-Prairie region (25%), followed by the Central Hardwood Region (17%). Decreases in oak relative density in these two regions were near universal (80% of the area for both regions, Table s2) and were particularly prominent on the Ozark Plateau, parts of the Cumberland Plateau, the western Highland Rim of Tennessee, and southern New England (Fig. 4a). Slightly over half of the areas in the Northern Hardwood Region and Southern Pine-Hardwood Region (55% and 60%, respectively) exhibited decreases in oak relative density.

Although the total volume of oak growing stock generally increased between T_1 and T_2, other species often increased even more, so that relative volume of oak species decreased in about 52% of the area of the eastern forest (Fig. 4b, Table s2). Both the Central Hardwood Region and Forest-Prairie Transition Region had significant decreases in oak relative volume (Table 2). In the Central Hardwood Region, over 73% of the forested area decreased in oak relative volume, with the sharpest declines occurring on the Ozark Plateau; the western portion of the Highland Rim; the Allegheny/Appalachian Plateaus in western Pennsylvania and New York, eastern Ohio, and West Virginia; the Coastal Plain of southern New Jersey; and the Driftless Section in Wisconsin and adjacent Minnesota. The only area in this region with prominent increases in oak relative volume was on the Cumberland Plateau and adjacent Ridge and Valley region of eastern Tennessee. In contrast, over 76% of the area in the Northern Hardwood Region increased in oak relative volume. Change in oak relative volume was mixed in the Southern Pine-Hardwood Region. East-central Mississippi and an adjacent portion of the Coastal Plain in northwestern Alabama had a sharp decrease in relative volume, while northern Georgia and a contiguous area in the Western Gulf Coastal Plain that centered on eastern Texas and adjacent portions of Louisiana and Arkansas had substantial increases in oak relative volume.

The spatial pattern for IV change is similar to that for relative volume (Fig. 4c). Again, the Central Hardwood Region and Forest-prairie Transition Region had significant decrease in oak IV (Table 2). Oak abundance increased on over 72% of the area in the Northern Hardwood Region, while oak abundance decreased on 81% of the area in the Central Hardwood Region. Within the Central Hardwood Region, the Ozark Plateau had the sharpest decrease in IV, and eastern Tennessee showed some increase. Increases and decreases in oak abundance in the Southern Pine-Hardwood Region were about evenly split by area.

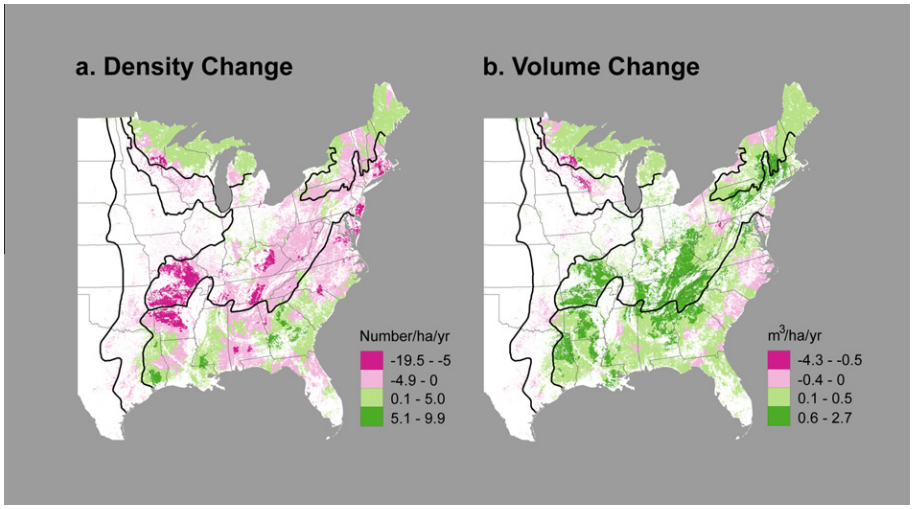

Fig. 3. Mean annual change in (a) density and (b) volume for all oak species in the eastern U.S. during the last two decades.

Table 2
Changes in oak relative density, relative volume, and IV between the first (T_1) and second (T_2) inventory during the last two decades by ecoregion.

Ecoregion	Rel. dens. (%)		Rel. vol. (%)		IV (%)	
	T_1	T_2	T_1	T_2	T_1	T_2
Northern Hardwood Region	4.5	4.4	10.7	11.5	7.6	7.9
Central Hardwood Region	14.1	11.7**	35.8	33.6**	24.9	22.7**
Southern Pine-Hardwood Region	15.9	15.3*	21.9	21.8	18.9	18.6
Forest-Prairie Transition Region	15.1	11.4**	37.6	32.8**	26.4	22.1**
All eastern forested area	14.0	12.4**	28.9	27.3**	21.4	19.9**

* Change during the study period is significant at $p < 0.05$.
** Change is significant at $p < 0.01$.

For all of the eastern U.S., regression of annual change in IV between T_1 and T_2 on IV at T_1 shows that IV tended to increase when the initial IV was low and decrease when it was high (Fig. 5). On average, counties with oak IV less than 15% at the first survey experienced an increase in IV, while counties with average oak IV greater than 15% experienced a decrease, and the higher the oak IV at T_1, the faster the rate of oak decline. Of all counties with <15% oak IV at T_1, 59% experienced an increase in oak abundance over the interval before the next survey, and of all counties with >15% oak IV at T1, 69% showed a decrease.

3.4. Change in relative abundance by species

Among all 25 species analyzed, approximately half (12) of them decreased significantly in relative density and only one species (water oak) increased significantly (Table 3). Five species decreased significantly in relative volume and five species increased significantly, and eight decreased significantly in IV while two increased (water oak and shingle oak). Both the top two most prevalent white oak species (white oak and post oak, as measured by the occurrence in number of counties) and red oak species (northern red oak and black oak) had significant decreases in density and overall abundance as expressed by IV.

Spatial distributions of IV change for the nine most prevalent oak species indicated that no species had universal increase or decrease of its abundance throughout its natural range (Fig. 6). This in itself is not surprising, but the spatial clustering of areas of increase or decrease indicates that changes were both non-random and non-local. About two-thirds of the area in white oak's natural range had some level of decline in abundance, and the decline was especially strong in northeastern Missouri and western-central Tennessee. But northern Georgia and central West Virginia had marked increases in white oak abundance, and some other portions of the range exhibited smaller increases (Fig. 6a). Post oak underwent widespread decreases in abundance (82% area) and the sharpest declines occurred in the Missouri Ozarks (Fig. 6b). Chestnut oak decreased in abundance in just over half (55%) of the areas in which it occurs, with the greatest decreases in eastern-central Kentucky, and the greatest increases in northern Georgia and eastern Tennessee (Fig. 6c). In contrast to the other white oak species, though, bur oak increased in abundance in nearly two-thirds of its natural range, especially in Minnesota (Fig. 6d).

Northern red oak, as the most prevalent red oak species, diminished in abundance in 58% of the area where it occurs (Fig. 6e). This species had the sharpest declines in southwestern Pennsylvania, northeastern West Virginia, northern Virginia, and southern Wisconsin and Michigan, but it gained markedly in abundance in the Upper Peninsula of Michigan and adjacent areas of Wisconsin and Minnesota as well as Maine and (interestingly) the Ozark Plateau (Fig. 6e). Black oak declined in three quarters of its natural range, with the greatest declines on the Ozark Plateau and on the Cumberland and Appalachian Plateaus in Kentucky (Fig. 6f). Scarlet oak had some level of decline in abundance over 64% of its range, but it became more abundant in northern Georgia, central and eastern Tennessee, and southeastern Kentucky (Fig. 6g). Southern red oak lost abundance in 59% of its native range, and most of the decrease occurred in the Coastal Plain (Fig. 6h). Water oak is one of the red oak species that had a near universal increase of its abundance throughout its native range (83% of area), and decreases were mostly restricted to the periphery of its range (Fig. 6i).

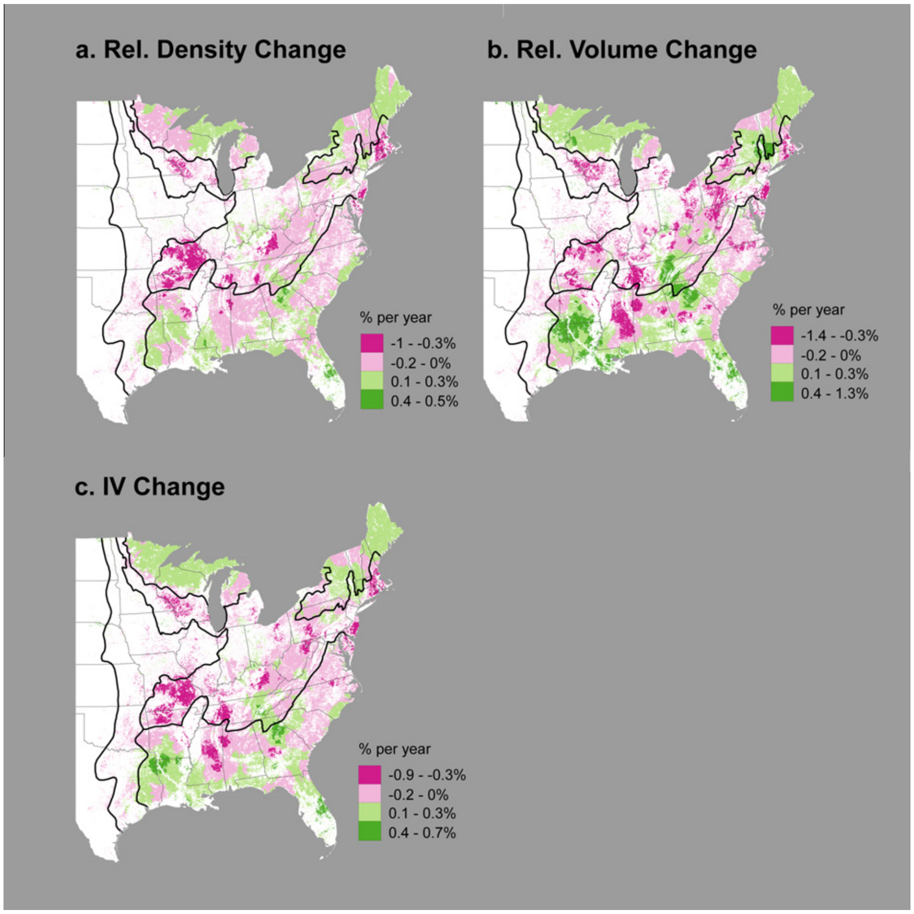

Fig. 4. Mean annual change in (a) relative density, (b) relative volume, and (c) importance value (IV) for all oak species in the eastern U.S. during the last two decades.

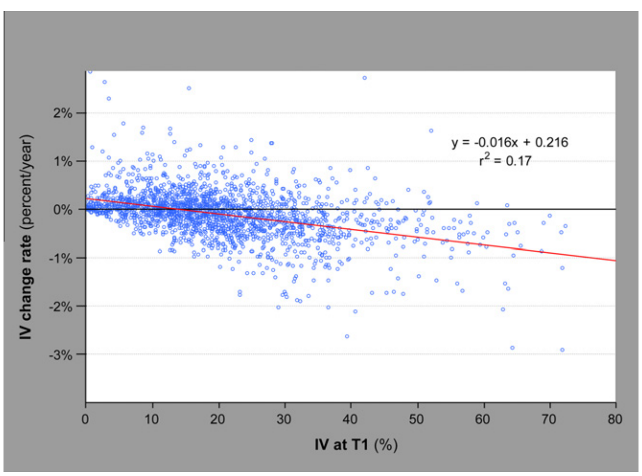

Fig. 5. Relationship between county level oak IV at T_1 and annual change in IV between T_1 and T_2.

4. Discussion

Our results show that trends in oak abundance in the eastern U.S. are complex, and every generalization is subject to caveats. Oak did, in fact, increase in volume in the eastern U.S., and in each of the four ecoregions, over the past two inventories. However, the majority of oak species, and most ecoregions, experienced a decline in the density of trees and especially the density of trees relative to other species. In addition, although oak volume generally increased, the changes were smaller and frequently negative when considered relative to other species. Thus, oak abundance as measured by IV declined for the last survey interval for most oak species and most ecoregions. Declines were especially marked in the Central Hardwood Region, which contains over half of the total volume of oak growing stock in the East. This region lost density on 87% of its forested area, relative density on 80%, relative volume on 73%, and IV on 81%. Declines in oak abundance have been reported for nearly 70 years or so (Lorimer, 1993). Our study confirms but adds nuance to the widespread impression that the eastern U.S. is losing oak: although oak is generally declining in both density and volume relative to other species, the absolute volume of oak growing stock still increasing, and some areas and some species show increases in relative density and volume.

The major exceptions to this general decline in oak abundance were (1) two species of red oak (water oak and shingle oak) that occur on moist sites in the South and Midwest and (2) large portions of the Northern Hardwood and Southern Pine-Hardwood Regions where oaks increased in both relative density and relative volume (although net changes were nil or negative for each region in its entirety). In addition, within the Central Hardwood Region, eastern Tennessee and an adjacent section of Georgia exhibited a gain in relative oak volume. It should be pointed out that although there appear to be density and volume gains for oak in the Northern Hardwood Region (Fig. 4), no changes were statistically significant. Also, this region contains only 6% of the volume of oak in the East. Thus, while contrary trends in this region may be of some ecological interest, oaks have much less economic importance, except perhaps locally, than in other regions. Gains in oak

Table 3
Changes in oak relative density, relative volume, and IV by species in the eastern U.S. between the first (T_1) and second (T_2) inventory during the last two decades (No. of counties = the number of counties in which a given species was present in the inventory record).

Species	No. of counties	Rel. dens. (%)		Rel. vol. (%)		IV (%)	
		T_1	T_2	T_1	T_2	T_1	T_2
White oak (*Q. alba*)	1739	3.4	2.8**	8.2	8.1**	5.8	5.4**
Post oak (*Q. stellata*)	1026	2.7	1.8**	3.7	3.1	3.2	2.5**
Chestnut oak (*Q. montana*)	636	3.0	2.8**	7.3	7.8	5.2	5.3
Bur oak (*Q. macrocarpa*)	623	4.2	4.4	9.9	11.9*	7.0	8.2
Chinkapin oak (*Q. muehlenbergii*)	594	1.1	1.3	2.2	2.4	1.7	1.9
Swamp chestnut oak (*Q. michauxii*)	466	0.4	0.3*	0.8	1.0*	0.6	0.7
Swamp white oak (*Q. bicolor*)	393	0.6	0.5	2.1	1.8	1.3	1.2
Overcup oak (*Q. lyrata*)	391	0.7	0.6*	1.7	2.1*	1.2	1.3
All white oaks (section *Quercus*)	**2033**	**6.7**	**5.5****	**14.7**	**14.4**	**10.7**	**9.9****
Northern red oak (*Q. rubra*)	1593	2.0	1.8**	6.4	5.7**	4.2	3.8**
Black oak (*Q. velutina*)	1487	2.1	1.8**	5.4	4.5**	3.8	3.2**
Scarlet oak (*Q. coccinea*)	959	1.2	1.0**	3.1	3.2	2.2	2.1*
Southern red oak (*Q. falcata*)	929	1.7	1.6*	2.8	3.0	2.2	2.3
Water oak (*Q. nigra*)	689	4.5	5.7**	3.9	4.7**	4.2	5.2**
Willow oak (*Q. phellos*)	592	1.1	1.0	2.2	2.1	1.6	1.6
Cherrybark oak (*Q.pagoda*)	522	0.6	0.6	2.0	2.4	1.3	1.5
Blackjack oak (*Q. marilandica*)	507	1.5	0.8**	1.1	0.6**	1.3	0.7**
Laurel oak (*Q. laurifolia*)	444	3.1	3.4	3.2	3.4	3.1	3.4
Pin oak (*Q. palustris*)	412	0.9	1.1	3.0	4.2	2.0	2.6
Shumard oak (*Q. shumardii*)	394	0.2	0.3	0.7	1.2	0.5	0.8
Shingle oak (*Q. imbricaria*)	279	1.7	2.2	2.0	2.8*	1.8	2.5*
Northern pin oak (*Q. ellipsoidalis*)	231	1.1	1.2	2.6	2.7	1.8	1.9
Nuttall oak (*Q. nuttallii*)	162	0.7	1.0	2.4	2.8	1.6	1.9
Live oak (*Q. virginiana*)	161	3.0	3.7	4.0	5.1	3.5	4.4
Turkey oak (*Q. laevis*)	146	3.9	2.3**	0.5	0.5	2.2	1.4**
Bluejack oak (*Q. incana*)	130	1.8	0.5**	0.4	0.1*	1.1	0.3**
All red oaks (section *Lobatae*)	**1998**	**8.1**	**7.8****	**15.8**	**15.0****	**12.0**	**11.4****

Bold indicates the sub-total statistics of all species in this section.
* Change during the study period is significant at $p < 0.05$.
** Change is significant at $p < 0.01$.

abundance within the South are largely attributable to the increased abundance of water oak.

In general, oaks have declined in abundance where they were most prevalent at T_1, and they have increased where they were previously uncommon. This was a stand-level phenomenon, not a species phenomenon. Areas where the density and/or volume of oak were initially low generally experienced an increase in oak abundance. But species that were uncommon at T_1, measured by volume or density, showed no particular tendency to become more abundant.

There has been concern that existing oak forests are aging, have insufficient oak regeneration, and lack sapling size oaks in the midstory (Abrams, 2003; Fei et al., 2005; McWilliams et al., 2002). McWilliams et al. (2002) reported that nearly half of the oak timberland is in the sawtimber size class and only a quarter in the seedling–sapling size class in the eastern U.S. Oak regeneration is often low in abundance and small in size, and it faces strong competition from other species (Fei et al., 2005). Heavy losses between the seedling and sapling stages of growth further limit the successful renewal and regeneration of the oak component in forests (Crow, 1988; Abrams, 2003). All of these successional phenomena are probably directly linked to the observed pattern of a general decline in oak abundance. However, it is unlikely that changes in abundance are uniform across size classes, and further regional analyses by size class with the partitioning of growth, ingrowth, and mortality are needed to fully grasp the current successional dynamic of oak forests.

Regional patterns of oak abundance change showed both conformity and differences among species, and gains and losses were strongly clustered in space. This clustering suggests that trends and counter-trends are caused by a variety of ecological or socio-economic factors operating at regional and sub-regional levels. Declines in overall oak abundance were especially pronounced on the Ozark Plateau; the Western Highland Rim of Tennessee; portions of the Cumberland and Appalachian Plateaus in Kentucky, West Virginia, and Pennsylvania; the Costal Plains Section of north-central Mississippi; and the Driftless Section of Wisconsin. Increases in overall oak abundance were pronounced in the Western Gulf Coastal Plain of Texas, Louisiana, and Arkansas; most of the Piedmont of northern Georgia; much of the Cumberland Plateau in Tennessee; and much of the Northern Hardwood Region, where increases in IV were widespread but not strong.

Many factors could be responsible for these distinct patterns of spatial consistency among different oak species. Regional vegetation patterns are, of course, the result of innumerable interrelated factors, including climate, geology, historic land use, topography, and disturbance (Ohmann and Spies, 1998). As we have shown, contrasting changes in relative density, relative volume, and IV tended to be associated with physiographic landforms as defined by coherent areas of geology and geomorphology. Thus, landform, which is closely related to vegetation type and the distribution and abundance of species, appears to correlate strongly with spatial patterns in the oak dynamic over the last two inventories, and the underlying causes are probably mediated by biological and ecological factors that cluster by landform. Other more directly anthropogenic factors, such as patterns of land ownership and land use, differences among local economies, historical differences in timber harvesting, variation in disturbance histories, and so on, may be responsible for the anomalies among species and across regions. Due to differences in biology, ecology, and economic importance among different species, the specific role each factor plays would vary among species and locations. However, the regional differences are intriguing and invite further analysis. For example, increases in IV were widespread (if not always strong) on the Piedmont of Georgia, but decreases in IV were almost ubiquitous on the Piedmont of Alabama, North Carolina, and Virginia. We know of no plausible ecological explanation for this fact, and presumably it is related to historical or contemporary socio-economic differences.

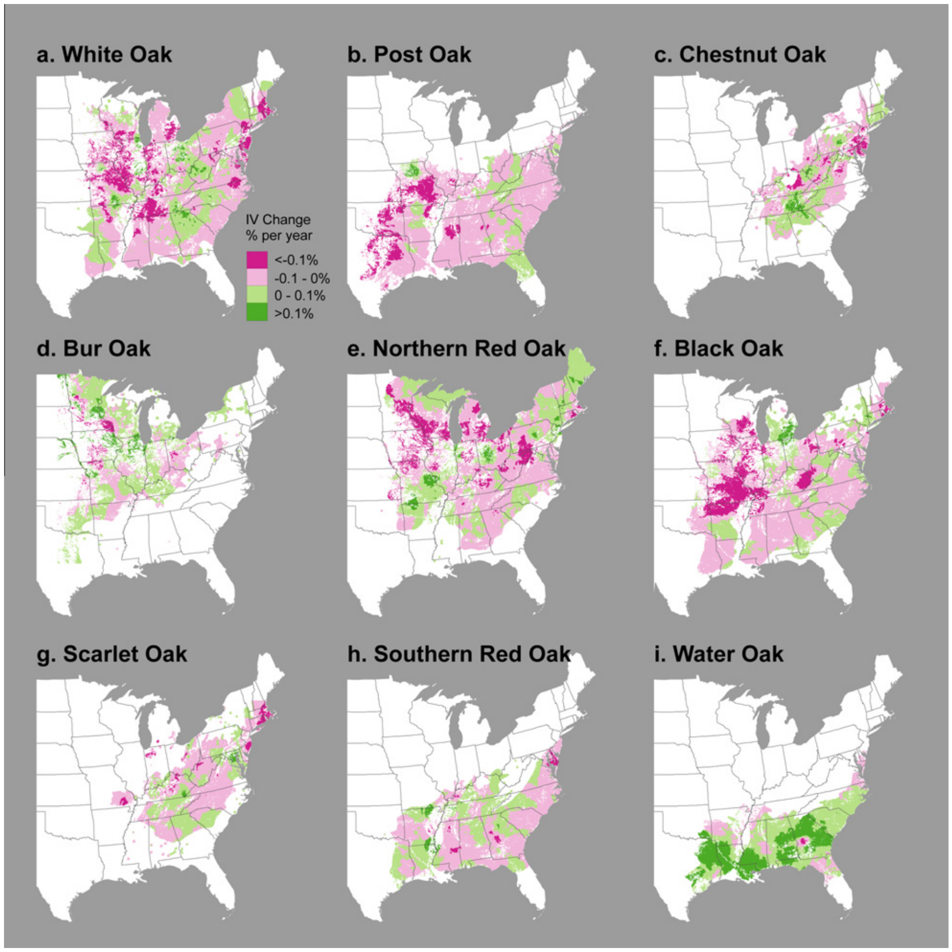

Fig. 6. Mean annual change in IV for the four most prevalent white oak species: (a) white oak, (b) post oak, (c) chestnut oak, and (d) bur oak; and five red oak species: (e) northern red oak, (f) black oak, (g) scarlet oak, (h) southern red oak, and (i) water oak within their natural distributions in forested area in the eastern U.S.

Thus, although oak is generally declining relating to associated species, the trend is not universal either regionally or among species, and the causes are probably varied and complex.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.06.030.

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