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Changing eastern broadleaf, southern mixed, and northern mixed forest ecosystems of the eastern United States

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ABSTRACT

Recognition of changes in forests provides greater perspective about current trajectories of forests. I compared the newest USDA Forest Service Forest Inventory and Analysis (FIA) surveys to the oldest available surveys in the eastern United States to detect increasing and decreasing species and groups over large spatial extents. Species appeared to be increasing at the expense of decreasing species within each of the major forest ecosystems of the eastern United States. In eastern broadleaf forests, oaks and Virginia pine are decreasing and maples and eastern redcedar are increasing. In southern mixed forests, planted loblolly and slash pine are replacing shortleaf and longleaf pines, and longleaf pine wetland associates of swamp tupelo, pond cypress, and pond pine. In northern mixed forests of the Great Lake states, quaking aspen and paper birch are decreasing whereas red pine, later successional black spruce and northern white-cedar, and maples of eastern broadleaf forests are increasing. Indeed, red maple now is more frequent than aspen in northern mixed forests. The historical legacy of fire continues to affect forest composition. Without fire, fire-tolerant oaks and pines (that are not planted) still are decreasing, whereas fire-sensitive tree species are increasing. Forestry practices benefit planted pines but are not as effective at supporting quaking aspen against competition from red maple and species of the eastern broadleaf forest as in the past.

1. Introduction

Identification of changes in forest composition provides information about current trajectories and potentially, future forests. Historically, presence and type of fire regime was a major determinant of forest types in the eastern United States. Open forest ecosystems of fire-tolerant oak or pine species covered most of the eastern United States, where indigenous cultures were agrarian and used frequent surface fire as a tool (Delcourt et al., 1998; Fuller et al., 1998; Lorimer, 2001; Cogbill et al., 2002; Black et al., 2006; Nowacki and Abrams, 2008; Hanberry et al., 2012a, 2012b). Regular stand-replacing fires (50–150 year return intervals) in northern mixed forests produced dense tamarack, aspen, and birch forests with variable densities of pine (Frelich and Reich, 1995; Hanberry et al., 2012b). In regions where there was not a fire regime, due to fire breaks or environmental limits on agriculture, mature forests of American beech (*Fagus grandifolia*; see Tables 1 and 2 for scientific names of other species), sugar maple, and eastern hemlock developed in eastern broadleaf forests, spruce and fir in northern mixed forests, probably American beech along with relatively long-lived species such as yellow-poplar (*Liriodendron tulipifera*) and sweetgum in southern mixed forests, and floodplain forests along riverways (Williams, 1989; Whitney, 1994; Hanberry et al., 2012c).

Forests in the eastern United States have changed during the past 100–200 years due to fire suppression, harvest, conversion to other land uses, introduction of exotic diseases, and deer herbivory. Oak and pine dominance have reduced in open oak or pine forest ecosystems because tree species that were formerly restricted to riparian forests and rocky outcrops expanded in distribution after effective fire suppression occurred during the 1920s (Nowacki and Abrams, 2008; Hanberry et al., 2012a). Furthermore, increased stem density converted open forests to closed forests and consequently, open forest ecosystems no longer exist at a landscape scale (Hanberry et al., 2012b; Hanberry et al., submitted for publication). Harvest and land use disturbance along with selection for other species have diminished the area of mature forests (Williams, 1989; Whitney, 1994). Harvest and drainage of floodplain forests followed by conversion to agriculture have replaced floodplain forests (Williams, 1989; Whitney, 1994; Hanberry et al., 2012c). Invasive species have reduced formerly common species such as American chestnut (*Castanea dentata*; Buchanan and Hart, 2012) and currently, are reducing eastern hemlock among other species (Fuller, 1998). Intensive deer herbivory appears to reduce many

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Table 1
Species (trees ⩾ 12.7 cm diameter) that increased or decreased in percent composition ⩾ 5% for ⩾ 2 million ha between oldest and newest USDA FIA surveys in the eastern United States. The first *p*-values, from paired *t*-tests, were for all ecological subsections, weighted by area, where the species was present with > 100 stems. The second *p*-values, also from paired *t*-tests for all ecological subsections, compared small trees (<12.7 cm in diameter) in old surveys to large trees in new surveys.

Species	Scientific name	Net change ha	Change % composition	Mean year old surveys	Mean year new surveys	*p*-value	*p*-value small trees
Loblolly pine	*Pinus taeda*	72704702	17.6	1974	2007	<.0001	<.0001
Red maple	*Acer rubrum*	29479009	7.4	1984	2006	<.0001	<.0001
Eastern redcedar	*Juniperus virginiana*	11049718	7.8	1982	2007	<.0001	0.1533
Slash pine	*Pinus elliotti*	10310840	11.8	1972	2006	0.064	0.0069
Green ash	*Fraxinus pennsylvanica*	7789190	8.7	1980	2007	0.2169	N/A
Boxelder	*Acer negundo*	5609990	11.4	1982	2007	0.0743	N/A
Red pine	*Pinus resinosa*	5128902	8.9	1983	2006	<.0001	N/A
Black spruce	*Picea mariana*	3128760	8.7	1980	2006	<.0001	0.0037
Northern white-cedar	*Thuja occidentalis*	2603295	10.1	1984	2006	0.0363	<.0001
Sugar maple	*Acer saccharum*	2132676	7.0	1987	2006	0.0011	0.1717
Tamarack	*Larix laricina*	2092218	10.3	1980	2006	0.0037	0.1632
Jack pine	*Pinus banksiana*	−2066916	−8.3	1979	2006	0.009	0.3393
Paper birch	*Betula papyrifera*	−2594284	−7.0	1982	2006	<.0001	0.1072
Eastern white pine	*Pinus strobus*	−3040918	−7.4	1986	2006	0.3578	0.3924
Virginia pine	*Pinus virginiana*	−5335089	−7.0	1979	2006	0.0004	0.4223
Pond pine	*Pinus serotina*	−5571550	−5.7	1972	2006	0.0005	N/A
Pond cypress	*Taxodium ascendens*	−5824112	−9.2	1970	2005	0.0015	N/A
American basswood	*Tilia americana*	−6116642	−7.0	1983	2006	0.0066	0.7936
Longleaf pine	*Pinus palustris*	−9881192	−8.0	1972	2007	<.0001	0.2804
Quaking aspen	*Populus tremuloides*	−12491657	−10.1	1979	2006	<.0001	<.0001
Black oak	*Quercus velutina*	−12661395	−8.3	1984	2007	<.0001	0.0002
Northern red oak	*Quercus rubra*	−14178855	−9.3	1984	2006	<.0001	0.0843
Swamp tupelo	*Nyssa biflora*	−14404729	−6.8	1972	2006	<.0001	0.0561
White oak	*Quercus alba*	−23820115	−7.6	1982	2006	<.0001	0.0325
Shortleaf pine	*Pinus echinata*	−38282915	−12.1	1975	2007	<.0001	0.1218

Table 2
Percent composition (trees ⩾12.7 cm diameter) of eastern forests by pines, other gymnosperms, oaks, other angiosperms, and most frequent species for oldest (mean year = 1981) and newest (mean year = 2006) USDA FIA tree surveys, as well as the percent composition of groups for smaller trees (<12.7 cm diameter) in newest surveys. The first *p*-values, from paired *t*-tests, were for all ecological subsections, weighted by area, where the group contained ⩾100 stems. See Table 1 for scientific names of increasing and decreasing species.

Forest type	Group	Old surveys		New surveys			*p*-value
		%	Most frequent	%	Most frequent	% Small trees	
Eastern broadleaf	Pines	7.4	Eastern white pine	8.0	Eastern white pine	4.3	0.0233
Eastern broadleaf	Other gymnosperms	3.1	Eastern hemlock, *Tsuga canadensis*	5.6	Eastern redcedar	5.5	<.0001
Eastern broadleaf	Oaks	38.2	White oak	26.6	White oak	9.5	<.0001
Eastern broadleaf	Other angiosperms	51.4	Red maple	59.8	Red maple	80.7	<.0001
Southeastern mixed	Pines	40.9	Loblolly pine	47.9	Loblolly pine	20.5	<.0001
Southeastern mixed	Other gymnosperms	3.6	Pond cypress	2.8	Pond cypress	2.3	0.0085
Southeastern mixed	Oaks	20.7	White oak	15.0	Water oak, *Quercus nigra*	16.1	<.0001
Southeastern mixed	Other angiosperms	34.8	Sweetgum, *Liquidambar styraciflua*	34.3	Sweetgum	61.1	0.0005
Northern mixed	Pines	7.7	Jack pine	8.9	Red pine	2.7	0.2194
Northern mixed	Other gymnosperms	25.9	Northern white-cedar	30.5	Northern white-cedar	37.2	<.0001
Northern mixed	Oaks	6.1	Northern red oak	4.8	Northern red oak	1.8	<.0001
Northern mixed	Other angiosperms	60.3	Quaking aspen	55.8	Red maple	58.3	<.0001
Prairies/savannas	Pines	1.9	Loblolly pine	3.0	Loblolly pine	2.3	0.0706
Prairies/savannas	Other gymnosperms	0.9	Eastern redcedar	4.4	Eastern redcedar	5.5	N/A
Prairies/savannas	Oaks	36.4	White oak	26.4	Post oak, *Quercus stellata*	13.8	<.0001
Prairies/savannas	Other angiosperms	60.8	American elm, *Ulmus americana*	66.2	American elm	78.5	<.0001
Prairies	Pines	4.0	Ponderosa pine, *Pinus ponderosa*	3.7	Ponderosa pine	2.0	N/A
Prairies	Other gymnosperms	3.2	Eastern redcedar	22.7	eastern redcedar	43.0	N/A
Prairies	Oaks	8.4	Bur oak, *Quercus macrocarpa*	11.5	Bur oak	4.1	N/A
Prairies	Other angiosperms	84.4	Eastern cottonwood, *Populus deltoides*	62.0	Green ash	50.9	0.4571

tree species in at least some localized areas (Royo and Carson, 2006).

Many species have increased in frequency within both historical and new distributions. Red maple, eastern redcedar, and quaking aspen are some of the species that have expanded distributions with a disturbance regime shift from fire to harvest (Abrams, 1998; Briggs et al., 2002; Fei and Steiner, 2007; Fei and Steiner, 2009; Hanberry et al., 2012a, 2012b). Loblolly pine and to some extent red pine, have increased due to silviculture, while non-favored pine species have decreased along with oaks (Cowell, 1995; Conner and Hartsell, 2002; Predmore et al., 2007; Pan et al., 2011; Hanberry et al., 2012d). Climate change will add another filter on tree species, perhaps favoring drought-tolerant species and reducing the gains that mesic species have made in sites that are xeric (Klos et al., 2009).

It can be difficult to recognize change that occurs over decades (i.e., 'the invisible present', Magnuson, 1990). Yet temporal contrasts provide the context necessary to recognize recent