



## Original article

# Advancement of tree species across ecotonal borders into non-forested ecosystems

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## ABSTRACT

Woody species are increasing in density, causing transition to more densely wooded vegetation states, and encroaching across ecotonal borders into non-forested ecosystems. We examined USDA Forest Service Forest Inventory and Analysis data to identify tree species that have expanded longitudinally in range, particularly into the central United States. We analyzed compositional differences within ecological regions (i.e., subsections) in eastern and western ranges of species using repeated measures ANOVA. We considered differences in outer ranges to indicate range expansion or contraction. We also estimated the shift in forest area and basal area relative to the center of the US and compared change in deciduous forest land cover. Out of 80 candidate species, 22 species expanded to the west, seven species expanded to the east, and five species expanded in both directions. During the survey interval, eastern tree species advanced into the predominantly non-forested ecosystems of central United States. Eastern cottonwood, eastern hophornbeam, eastern redbud, honeylocust, Osage–orange, pecan, red mulberry, and Shumard oak represent some of the species that are advancing eastern forest boundaries across forest-grassland ecotones into the central United States. Forest land has shifted towards the center of the continent, as has the center of mean tree basal area, and a simple comparison of deciduous cover change also displayed forest advancement into the central United States from eastern forests. The expanding species may spread along riparian migration corridors that provide protection from drought. Humans use the advancing tree species for windbreaks, fencerows, and ornamental landscaping, while wildlife spread fruit seeds, which results in unintentional assisted migration, or translocation, to drier sites across the region.

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## 1. Introduction

Woody species have increased in stem density (i.e., densification), causing a shift in state from open forest ecosystems of savannas and woodlands to closed forests, while also expanding across ecotonal boundaries into non-forested ecosystems (Hanberry et al., 2014). Woody encroachment by shrubs into grasslands has been documented in North America, Australia, Africa, Asia, and Europe (Eldridge et al., 2011; Komac et al., 2013). Tree species additionally are crossing ecotonal boundaries into non-forested ecosystems. Advancement of tree species has occurred in North America, Australia, Africa, Asia, and South America (e.g., Kaye et al., 2010; Mitchard et al., 2011).

In the United States, transitions are in progress as ecosystems become increasingly more wooded. This probably is due to different disturbance regimes including exclusion of frequent, low intensity surface fires and changes in grazing and management practices, generally either to more intensive or more severe yet less frequent disturbance, as well as tree and shrub planting. However, there certainly are multiple additional drivers of increasing and expanding tree species, particularly changing precipitation. In any event, shrub- and grasslands of the central United States are being invaded by tree species of the eastern and western United States (Abrams, 1986; Briggs et al., 2002; Kaye et al., 2010). Currently, the predominant advancing tree species are fire-sensitive junipers, which do not have adaptations to survive fire and in some cases have had assisted migration as planted windbreaks (Briggs et al., 2002; Hanberry et al., 2014). Ponderosa pine (*Pinus ponderosa*) additionally was an early colonizer into the central United States (Brown and Seig, 1999; Kaye et al., 2010; Hanberry et al., 2014). The

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central United States contains stream networks that provide migration corridors for broadleaf tree species, such as willows and cottonwoods, as well as junipers (Abrams, 1986; Johnson et al., 2012). Exclusion of flooding has allowed riparian forests to remain established and advance to uplands (Loehle et al., 1996; Johnson et al., 2012).

In addition, numerous tree species are densifying, or increasing in number of stems, within historically open forested ecosystems of savannas and woodlands (Hanberry et al., 2014). In the eastern United States, open longleaf pine ecosystems dominated sandy soils of the Coastal Plain along the Gulf Coast and Atlantic Ocean from Texas to Virginia. Open pine ecosystems extended up the Atlantic coast as pine barrens, which probably continued at least as scattered ecosystems with an oak and eastern broadleaf forest matrix until meeting the colder northern mixed forests in New England (Cogbill et al., 2002). In the interior, between the grasslands of the central US and forests of the eastern US, open oak

ecosystems stretched from Texas into Canada. Similarly to pine barrens, open oak ecosystems probably ranged east to the Atlantic Coast, although closed eastern broadleaf forests became dominant as disturbances changed spatially (Morgan, 1975; Whitney and Decant, 2003). Most of the eastern United States contains records of frequent surface fire regimes because pre-industrial societies used fire as a tool (Hart and Buchanan, 2012). After effective fire exclusion began in the 1920s, fire-sensitive species of eastern broadleaf forests and southern mixed forests have become abundant in open oak and pine ecosystems, to the extent that historical savannas and woodlands are now relicts (Hanberry et al., 2014). Moreover, recent afforestation of eastern grasslands has been recorded since the 1920s (Gleason, 1922).

Correspondingly, many lower elevation forests in the western United States were dominated by open ponderosa pine ecosystems, with some open oak ecosystems in Mediterranean provinces of California and valleys and foothills of the Southwest and Northwest

**Table 1**

Summary of the number of forest plots by state for each survey with information about the extent of the old survey data by state.

State	New surveys				Old surveys		Plots added to old surveys from new surveys	Footnote
	Forest area (million ha)	Survey intensity (ha per plot)	Count of forest plots	Years	Count of forest plots	Years		
AL	9.3	2412	4258	2005–2012	3753	1971–1972	11	a
AZ	7.5	2505	3181	2003–2012	719	1981–1985	2664	a
AR	7.6	2421	3544	2007–2012	2935	1977–1979	35	a
CA	13	2637	5529	2003–2012	1153	1991–1994	4336	d
CO	9.2	2534	3948	2003–2012	721	1979–1997	2038	a
CT,DE,MA,RI	2.1	2510	1136	2008–2013	523	1984–1985	23	a
FL	7	2464	3198	2001–2013	4798	1968–1970	269	a
GA	10	2425	4651	2004–2012	6301	1970–1972	45	a
ID	8.6	2734	3384	2004–2012	2218	1981–1998	1376	a
IL	2	2519	1032	2007–2012	1095	1982–1985	63	a
IN	1.9	1294	1988	2007–2013	1998	1985–1987	32	a
IA	1.2	2580	645	2007–2012	626	1989–1990	29	a
KS	1	2572	610	2008–2013	937	1980–1981	24	a
KY	5	2445	2467	2005–2012	1927	1986–1998	23	a
LA	6	2454	2709	2000–2013	2510	1972–1974	11	a
ME	7.1	2399	3170	2007–2012	2630	1994–1996	67	a
MD	1	2734	452	2008–2013	653	1985–1986	25	a
MI	8.1	2304	4001	2007–2012	7998	1974–1984	123	a
MN	7	1288	6224	2007–2012	8903	1974–1980	348	a
MS	7.9	2427	3668	2005–2013	2807	1976–1977	8	a
MO	6.3	2389	3161	2007–2012	4671	1987–1989	82	a
MT	10.3	2509	4451	2003–2012	3239	1988–1998	1070	a
NE	0.6	2632	333	2007–2013	159	1982–1983	22	a
NV	4.3	2647	1737	2004–2012	61	1979–1997	1683	a
NH,VT	3.8	2467	1740	2008–2013	1206	1982–1983	85	a
NJ	0.8	2618	367	2008–2013	250	1986–1987	21	a
NM	10	3081	3444	2008–2012	323	1986–1987	2797	a
NY	7.6	2674	3302	2008–2013	2956	1991–1994	464	a
NC	7.5	2406	3668	2003–2012	5101	1973–1975	75	a
ND	0.3	2450	186	2008–2012	145	1978–1979	66	a
OH	3.3	2503	1661	2008–2013	1652	1990–1991	46	a
OK	5.1	3821	1668	2007–2013	1075	1985–1990	514	a
OR	12	1361	9450	1999–2012	1435	1995–1998	7805	e
PA	6.7	2655	2974	2008–2013	2971	1988–1990	85	a
SC	5.3	2408	2498	2007–2012	4329	1966–1968	15	a
SD	0.8	2446	375	2008–2012	288	1980–1995	184	c
TN	5.6	2437	2709	2005–2013	2169	1979–1980	70	a
TX	24.9	3346	8218	2004–2013	1990	1974–1976	5989	b
UT	7.3	2512	3176	2003–2012	1228	1988–1995	2491	a
VA	6.4	2393	3035	2008–2013	4221	1975–1977	103	a
WA	8.9	1635	5917	2003–2012	900	1996–2001	3794	d
WV	4.9	2695	2016	2008–2013	2545	1987–1989	69	a
WI	6.9	1254	6363	2007–2012	6887	1981–1984	81	a
WY	4.2	12,635	366	2011–2012	365	1983–1992	174	a

<sup>a</sup> Old surveys in these 44 states sampled only timberlands.

<sup>b</sup> 1975 Texas sampled only timberlands and did not sample any lands in West Texas.

<sup>c</sup> 1980 South Dakota survey sampled only timberlands and did not sample any lands west of the 103rd meridian.

<sup>d</sup> 1994 California and 2001 Washington surveys sampled only timberlands and did not sample any federal lands managed by the USDA Forest Service.

<sup>e</sup> 1999 Oregon surveys sampled only timberlands and did not sample any federal lands managed by the USDA Forest Service or USDI Bureau of Land Management.

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