

# Long-term directional changes in upland *Quercus* forests throughout Oklahoma, USA

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## Abstract

**Questions:** (1) How have the composition and structure of undisturbed upland *Quercus* forests changed over 50 years across a large region and moisture gradient; (2) What factors are associated with long-term and broad-scale changes in these forests?

**Location:** Oklahoma, USA.

**Methods:** We re-sampled 30 forest stands originally sampled in the 1950s across a large geographical area and compared basal area, tree density, and sapling density between the sampling periods using paired *t*-tests, CCA, and DCA. We examined vegetation dynamics in the context of drought indices compiled for the sample period.

**Results:** Total and *Quercus stellata* basal area and tree density increased, but *Q. stellata* and *Q. marilandica* sapling density decreased. *Juniperus virginiana* and woody species richness increased for all measures. DCA indicated that re-sampled stands generally changed from *Q. stellata*–*Q. marilandica*-dominated forests to forests with greater woody species richness and more *J. virginiana*. *Q. stellata* remained a dominant tree species; otherwise, composition shifted towards mesophytic and invasive woody species. Measurements taken in the 1950s immediately followed a major drought; whereas subsequent decades were significantly moister.

**Conclusions:** Fire exclusion and drought may have played an important role in driving changes towards lower dominance by *Quercus*, increased importance of mesophytic and invasive species, and greater woody species richness. These phenomena are

similar to those found in *Quercus*-dominated forests throughout the northern hemisphere.

**Keywords:** Drought; Fire exclusion; Forest dynamics; *Juniperus virginiana*; mesophication; Oak; Oklahoma; *Quercus marilandica*; *Quercus stellata*; Species composition; Vegetation change.

**Nomenclature:** Kartesz (1999).

**Abbreviations:** CCA = Canonical Correspondence Analysis, DCA = Detrended Correspondence Analysis, NMDS = Non-metric Multidimensional Scaling, PDSI = Palmer Drought Severity Index.

## Introduction

Anthropogenic changes in disturbance regimes have altered forest composition and structure worldwide (Abrams 1992; Donaubauer 1998; Sonesson 1999). Recent research suggests that fire exclusion can alter stand structure and create microclimatic conditions that are more beneficial to mesophytic woody species than to *Quercus* (Oak et al. 1996; Thomas et al. 2002). This can lead to rapid replacement of *Quercus* in mesic forests, but this process may be slower and transitory in xeric forests since there are substantially fewer woody species available to replace *Quercus* (Nowacki & Abrams 2008).

In south-central North America, disturbances such as fire, drought, and windstorms play an important role in the structure and composition of xeric *Quercus* forests (Hoagland et al. 1999; Shirakura et al. 2006). These disturbances benefit early successional, shade-intolerant, fire-tolerant vegetation such as *Quercus* (Clark 1993; Abrams 2003; McDonald et al. 2003). However, the combination of these disturbances with opportunistic fungal pathogens (*Armillaria* spp., *Hypoxylon* spp., and *Phytophthora* spp.) may have negative effects on *Quercus* (Brasier 1996; Wargo 1996). Fire exclusion in prairie and savanna ecosystems of south-central North America benefits the fire-intolerant invasive *Juniperus virginiana* (Bragg & Hulbert 1976) and may affect adjacent *Quercus* forests.

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*Quercus* is the most abundant and widespread hardwood genus in the northern hemisphere and accounts for more than twice the basal area of any other genus of hardwood in the United States (Arno 1995). Globally, many *Quercus* forests are in a state of transition to other dominant species (Sonesson 1999; von Oheimb & Brunet 2007). Therefore, understanding mechanisms of species change in these ecosystems is crucial. Long-term and broad-scale studies are useful for characterizing forest stand dynamics. However, there is a paucity of studies in forest ecosystems that are both long term (Arévalo et al. 2000; Foster & Aber 2004; Schuler 2004) and broad scale (Shifley et al. 2006). In addition, studies describing patterns of species change in *Quercus* forests are rare (Chapman et al. 2006; Rogers et al. 2008).

We took advantage of an opportunity to re-sample xeric upland *Quercus* forests located throughout Oklahoma, USA, 50 years after initial measurement in order to determine how composition and structure changed. In this paper, we document long-term and broad-scale changes to xeric *Quercus* forests in south-central North America and present evidence that the changes and their causes may be related to those reported for many mesic *Quercus*-dominated ecosystems.

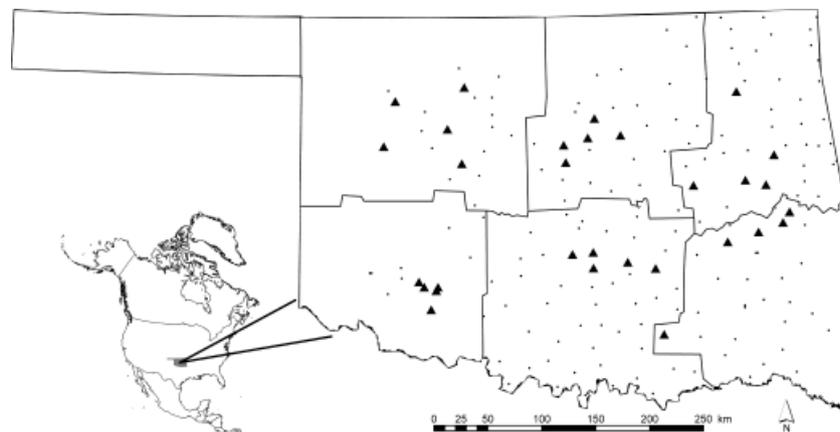
## Methods

### Study area

In south-central North America, a 4.8 million hectare mosaic of prairie, oak savanna, oak woodland, and oak forest ranges across parts of Kansas,

Arkansas, Oklahoma, and Texas, USA (Duck & Fletcher 1943; Kùchler 1964). This area is an ecotone between deciduous forests to the east and prairie ecosystems to the west, north, and south (Hoagland et al. 1999). Mean annual temperature and growing season length ranges from 15°C and 180 days in the north, to 19°C and 240 days in the south (Court 1974; Bell & Hulbert 1976). Mean annual precipitation ranges from 71 cm in the west to 102 cm in the east, nearly half of which falls during the spring months (Sutherland 1977). Elevation decreases from approximately 700 to 200 m a.s.l. from west to east, and forest ecosystems persist on both flat and exceedingly steep terrain. Prairie vegetation typically occurs on limestone and shale-derived parent material with fine-grained clay soils, while forest and savanna vegetation typically occurs on sandstone-derived parent material with coarse-grained sandy soils (Dyksterhuis 1948; Bell & Hulbert 1976; Powell & Lowry 1980; Rhodes 1980). Forests, woodlands, and savannas are characterized by *Q. stellata* and *Q. marilandica*, with *Carya* spp. subdominant in the east and *J. virginiana* subdominant in the west (Dyksterhuis 1948; Johnson & Risser 1972; Hoagland et al. 1999).

E.L. Rice & W.T. Penfound sampled the woody vegetation of 209 upland forest stands between 1953 and 1957. These stands varied in size from 16 to 259 ha, and were distributed across six regions of Oklahoma, excluding the far western “panhandle” (Kelting & Penfound 1953; Rice & Penfound 1959 and Fig. 1). In 2007 and 2008, we located five of these stands in each of the six regions by legal description and hand-drawn maps of the shape and location of each stand provided on Rice & Penfound’s datasheets. We chose stands that were



**Fig. 1.** Location of re-sampled (triangles) and non-re-sampled (dots) forest stands originally sampled by Rice & Penfound (1959) in Oklahoma, USA. Solid lines within the state indicate the six regions where the forest stands were located.

included in the Postoak–Blackjack Forest Type (Duck & Fletcher 1943) for the purpose of re-sampling upland *Quercus* forests. This excluded any forestland considered bottomland or non-*Quercus*-dominated in the 1940s and 1950s (Rice & Penfound 1959). The 30 forest stands selected for re-sampling were sampled from July to August of 1953 and 1956, and re-sampled from May to October of 2007–2008. They were chosen because they appeared to be the least anthropogenically disturbed of the remaining stands in each region (i.e., no paths cleared or vegetation removed). We assessed this from aerial photographs, ground-truthing, and discussion with landowners and lessees to corroborate land ownership and possible changes in land use since the 1950s. We carefully confined sampling to areas clearly within Rice and Penfound's original stands. Rice and Penfound's notes indicated that all of the re-sampled stands had burned frequently and recently prior to the 1950s sampling period. In 2007 and 2008, careful observation and information provided by landowners and lessees suggested that the re-sampled stands had no recent history of fire.

#### *Vegetation sampling*

We collected data on woody vegetation using the same methods as Rice & Penfound (1959). No herbaceous inventory was undertaken in either the 1950s or 2000s. In each intact stand, we used 40 prism plots spaced approximately 22 m apart throughout the forest interior to measure tree basal area [woody stems >7.62-cm diameter at breast height (DBH)] per plot by species using a BAF10 prism (Avery & Burkhart 1994). Between each of these plots, we used a 1.83-m wide by 22-m long plot to count the number of tree (>7.62-cm DBH) and sapling (2.54–7.62-cm DBH) stems per plot, by species. From these data, we estimated tree basal area, tree density, and sapling density. In stands that were too small or contained anthropogenically disturbed portions, we used fewer plots and confined data collection to undisturbed areas. For more information on data collection methods, see Rice & Penfound (1955, 1959).

#### *Environmental variables*

To determine the incidence of drought in south-central North America from the 19th to 21st centuries, reconstructed PDSI was used from an average of grid points 163 (100.0°W 37.5°N), 178 (97.5°W 37.5°N), 192 (95°W 37.5°N), 164 (100.0°W

35.0°N), 179 (97.5° W 35.0° N) and 193 (95°W 35°N) for the years 1800–2003 (Cook et al. 2004). Under this system, a value of  $-4$  is considered extreme drought and  $4$  extremely wet (Palmer 1965). Although more current PDSI data exist, these were not available at the fine spatial scale that the aforementioned grid points provided after 2003.

Soil data were taken from the USDA NRCS Web Soil Survey (Soil Survey Staff 2009) and climate data were provided by the Oklahoma Mesonet (2008).

#### *Data analysis*

For all analyses, the experimental unit was the forest stand, with sub-sample plots measured within each stand.

We used paired Student's *t*-tests separately on stand means of all three measures to determine whether differences in basal area ( $\text{m}^2 \text{ha}^{-1}$ ), tree density ( $\text{trees ha}^{-1}$ ), sapling density ( $\text{saplings ha}^{-1}$ ) and woody species richness between the 1950s and 2000s sampling periods differed significantly from zero.

We used CCA (ter Braak 1986) on stand means of all three measures to determine the effect of regional environmental gradients and soil on woody species composition. The environmental data we used for each stand included geographic coordinates, elevation, mean annual temperature, and precipitation; soil data included depth to any soil restrictive layer, depth to water table, pH, percentage clay, sand and silt, and the drainage class (Oklahoma Mesonet 2008; Soil Survey Staff 2009). Significance was assessed at  $P < 0.05$ .

We performed both NMDS (Kruskal 1964a, b; Mather 1976) and DCA (Hill & Gauch 1980) separately on stand means of all three measures to determine shifts in species composition over time. Results of DCA and NMDS were qualitatively similar and illustrated the same spatial and temporal trends. Because DCA produces simultaneous species and sample scores, and scales samples according to units of beta diversity, we found the results more readily interpretable and therefore display the DCA results here. We used DCA on all 1950s stand means as well as stand means from the 30 stands re-sampled in the 2000s for all three measures to clarify the directions of woody species change after accounting for all intersite variation. All data used in the DCAs were relativized and square-root transformed (Sokal & Rohlf 1995), and all multivariate analyses were performed with CANOCO 4.5 (ter Braak & Šmilauer 2002).

**Results**

*Q. stellata* and *Q. marilandica* accounted for the majority of trees and saplings in the 1950s, but their sapling densities decreased dramatically in the 2000s (Table 1). The combined *Q. stellata* and *Q. marilandica* component decreased from 84% to 67% of the basal area, from 82% to 61% of the tree density, and from 72% to 26% of the sapling density over 50 years. Woody species richness increased between sampling periods for both trees (4.5 to 7.5,  $P < 0.001$ ) and saplings (4.0 to 6.5,  $P < 0.001$ ) (data not shown). Separate CCAs (not shown) revealed a strong precipitation effect for all three measures. None of the other environmental variables had a significant effect. Total basal area increased by over 94% and total tree density by over 71% (Fig. 2). All three DCA biplots exhibited a longitudinal gradient on Axis 1 (left to right corresponded with west to east) and a time gradient on Axis 2 (Fig. 3). All three DCA biplots showed a general compositional shift away from *Q. stellata* and *Q. marilandica* with a greater decrease in dominance for *Q. marilandica*.

*Basal area*

DCA of basal area generally showed a compositional shift towards a number of more mesophytic species (e.g., *Ulmus* spp.) and *J. virginiana* (Fig. 3a). *Carya texana*, *J. virginiana*, *Morus rubra*, *Q. stellata*, and total basal area increased between sampling periods (Table 1, Fig. 2).

*Tree density*

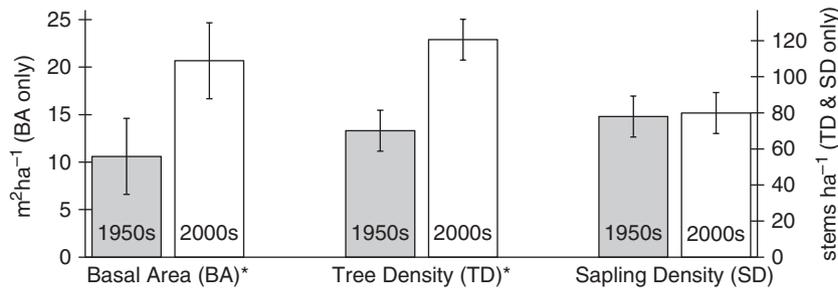
DCA of tree density generally showed a shift towards more mesophytic species (e.g., *M. rubra*, *Celtis laevigata*) and *J. virginiana* (Fig. 3b). *C. texana*, *Ce. laevigata*, *J. virginiana*, *M. rubra*, *Q. stellata*, *U. alata* and total tree density increased between sampling periods (Table 1, Fig. 2).

*Sapling density*

DCA of sapling density showed a compositional shift towards *J. virginiana* (Fig. 3c). Additionally, western and central stands showed increases in wes-

**Table 1.** Tree basal area and density, and sapling density for selected species in the 1950s and 2000s in upland *Quercus* forests of Oklahoma, USA (standard error in parentheses). An asterisk indicates a statistically significant change ( $P < 0.05$  from paired Student's *t*-tests).

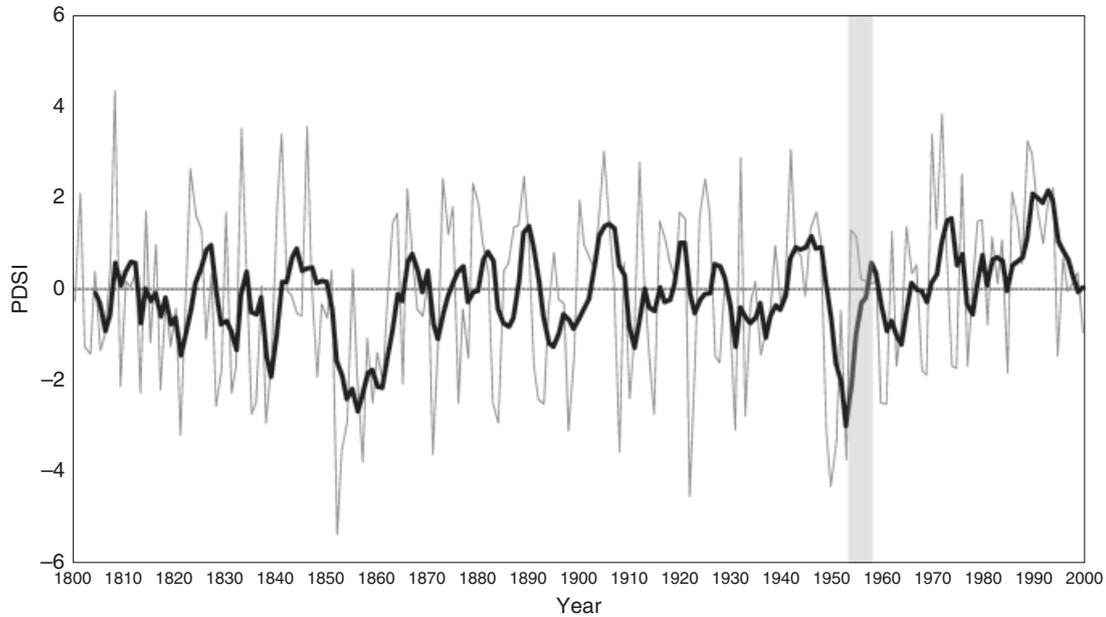
Species	Trees				Saplings	
	Basal Area ( $m^2 ha^{-1}$ )		Density (stems $ha^{-1}$ )		Density (stems $ha^{-1}$ )	
	1950s	2000s	1950s	2000s	1950s	2000s
<i>Carya texana</i>	0.42 (0.11)	1.32 (0.36)*	3.16 (0.86)	7.91 (2.33)*	3.81 (1.39)	7.00 (2.19)
<i>Celtis laevigata</i>	<0.01 (<0.01)	0.09 (0.06)	0	0.84 (0.37)*	0.06 (0.04)	1.54 (0.56)*
<i>Cornus drummondii</i>	0	0	0	0	0	2.34 (1.05)*
<i>Juniperus virginiana</i>	0.05 (0.03)	2.71 (0.78)*	0.73 (0.33)	23.85 (7.53)*	0.41 (0.19)	18.76 (4.90)*
<i>Morus rubra</i>	<0.01 (<0.01)	0.07 (0.03)*	0	0.60 (0.22)*	0.07 (0.07)	1.36 (0.44)*
<i>Quercus marilandica</i>	3.15 (0.47)	2.89 (0.55)	25.43 (4.50)	20.91 (4.76)	23.06 (4.59)	9.87 (3.19)*
<i>Quercus stellata</i>	5.72 (0.72)	11.07 (1.22)*	34.41 (3.84)	50.07 (5.93)*	38.56 (8.33)	11.23 (1.90)*
<i>Sideroxylon lanuginosum</i>	0.04 (0.02)	0.10 (0.05)	0.23 (0.17)	1.18 (0.59)	0.35 (0.14)	1.47 (0.39)*
<i>Ulmus alata</i>	0.14 (0.05)	0.26 (0.09)	0.81 (0.32)	3.85 (1.35)*	2.46 (0.83)	6.13 (1.69)*



Asterisks indicate statistically significant changes ( $p < 0.05$  from paired Student's *t*-tests).

**Fig. 2.** Changes in total basal area, tree density and sapling density between the two sampling periods in upland *Quercus* forests of Oklahoma, USA (error bars represent SE).





**Fig. 4.** Average annual PDSI for south-central North America with 5-year moving average. Shaded vertical bar indicates the 1950s sampling period. Adapted from Cook et al. (2004).

*Quercus* forests by enabling later-successional, shade-tolerant, fire-intolerant species to proliferate (Lorimer 1985; Rogers et al. 2008). Fire exclusion in mesic environments may also promote microclimatic conditions favoring mesophytic woody species over *Quercus*. However, previous studies suggest that fire exclusion does not have the same effect in xeric *Quercus* forests due to *Quercus* physiological adaptations to drought and the scarcity of later-successional woody species with high drought tolerance (Abrams 1990; Nowacki & Abrams 2008).

Following European settlement and the subsequent decline of indigenous populations, the use of fire decreased in south-central North America (Abrams 1986), often leading to changes in dominance in *Quercus*-dominated ecosystems (Abrams & Downs 1990; Abrams 1992; Wolf 2004). In many cases, decreases in fire frequency considerably altered vegetation types in little more than one century (Bragg & Hulbert 1976; Collins & Adams 1983; Jessup et al. 2003; Chapman et al. 2006). In the forest stands we re-sampled, changes in woody species composition were probably associated with canopy closure. This probably created less suitable conditions for shade-intolerant species like *Quercus* by altering light conditions in previously more open-canopy forests (Peterken 1996; von Oheimb & Brunet 2007; Peterson et al. 2007).

Rice and Penfound collected their data towards the end of the worst drought in recent history

(Rice & Penfound 1959; Cook et al. 2004, 2007 and Fig. 4). While *Quercus* is generally drought-tolerant (Abrams 1990), the severity of the 1950s drought may have reduced basal area and tree density below the potential of these forest stands during the mid-to-late-1950s. Total basal area and tree density may have increased between the 1950s and 2000s due to the post-drought recovery of woody vegetation and the absence of fire. This may suggest widespread conversion of open to closed-canopy *Quercus* forests occurred after the 1950s (Penfound 1962; Johnson & Risser 1975).

The factors responsible for increases in basal area and tree density apparently did not affect saplings in the same way since total sapling density remained unchanged after 50 years. *Quercus* regeneration is strongly stimulated by fire whereas the mesophytic and invasive woody species found in these stands are hindered by fire (Penfound 1968; Briggs et al. 2002; McEwan et al. 2007). *Q. marilandica* and *Q. stellata* sapling density decreased, which may suggest a future decline in *Quercus* spp. as they are slowly replaced by fire-sensitive mesophytic and invasive species such as *C. texana*, *J. virginiana* and *U. alata*.

Fire history studies in *Quercus*-dominated forests of south-central North America generally suggest that fire frequency and/or severity decreased during the 20th century (Clark et al. 2007; Stambaugh et al. 2009). Overgrazing, clearing for

agriculture, and urbanization likely reduced the fire frequency due to fine fuel reduction and fire suppression (Fuhlendorf & Smeins 1997). In our study sites, this could have decreased *Quercus* reproduction over the last 50 years and improved conditions for mesophytic and invasive species, which in turn have less flammable litter than *Quercus*.

Although sapling density of both *Q. stellata* and *Q. marilandica* decreased, they otherwise exhibited different changes over 50 years. *Q. stellata* trees maintained dominance, but *Q. marilandica* trees declined in dominance due to both decreasing populations of *Q. marilandica* and increases in other species (especially *J. virginiana*). In addition, *Q. marilandica* is associated with forest edge habitats, an indication that it needs a high light environment not provided in closed stands such as those sampled in the 2000s (Arévalo 2002). Generally, red oaks (section *Lobatae*, including *Q. marilandica*) are more susceptible to drought and fire mortality, more affected by pathogens, shorter lived, and less shade tolerant than white oaks (section *Quercus*, including *Q. stellata*) (Menges & Loucks 1984; Jenkins & Pallardy 1995; Huddle & Pallardy 1999; Johnson et al. 2002).

According to Rice & Penfound (1959), *Q. marilandica* was more affected by drought than any other tree species in the 1950s sampling period. We observed high *Q. marilandica* mortality in conjunction with *Hypoxylon* spp. and high densities of *J. virginiana* saplings and trees in many stands (data not shown). Rapid *J. virginiana* establishment appeared to follow *Q. marilandica* senescence in these stands. The incidence of severe and prolonged drought prior to and during the 1950s sampling period (Cook et al. 2004, 2007 and Fig. 4), combined with decreased fire may explain decreases in *Q. marilandica* and an increase in *J. virginiana*. While *J. virginiana* encroachment in rangelands has been well documented (Briggs et al. 2002), we believe our data are the first to show a long-term and large-scale increase of this species in forests.

*Quercus*-dominated forests studied here appear to be in transition to closed-canopy mesophytic forest stands with less *Quercus* and more shade-tolerant tree species. We found evidence to implicate drought and a decrease in fire in the alteration of woody species composition (Pallardy et al. 1988; McEwan et al. 2007; Hutchinson et al. 2008). Future stands may have less flammable litter due to more mesophytic woody species, perpetuating the positive feedback loop of mesophication and further worsening the conditions for *Quercus* (Nowacki & Abrams 2008). Additionally, a substantial increase

in *J. virginiana* will likely change wildlife communities and hydrology (Horncastle et al. 2005).

Broad-scale changes in woody species composition towards more mesophytic character occur in *Quercus* forests globally; our study shows that relatively rapid directional changes can occur in both mesic and xeric *Quercus* forests.

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## Supporting Information

Additional supporting information may be found in the online version of this article:

**Appendix S1.** Complete woody species list for sampled species > 2.54 cm DBH for upland *Quercus* forests of Oklahoma for the 1950s and 2000s sampling periods.

**Appendix S2.** 2007 photograph of re-sampled forest stand originally sampled by E.L. Rice and W.T. Penfound (1959) in Oklahoma, USA.

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