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Overstory species response to clearcut harvest across environmental gradients in hardwood forests

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ABSTRACT

Despite their long history as a forest dominant, the importance of *Quercus* (oak) species is declining under contemporary disturbance regimes in many parts of the world. This is cause for concern considering the great economic and ecological value of this genus. While many chronosequence studies have shown that clearcutting has accelerated the loss of *Quercus* species in forests of eastern North America, long-term repeated measures studies are needed to understand how topo-edaphic variables and disturbance history influence the persistence of the genus in post-harvest stands. In 1988, a study was implemented on the Hoosier National Forest (HNF) in southern Indiana, USA to examine the fate of *Quercus* species and their competitors within developing stands following clearcut harvests. Permanent plots were established in six harvest units in *Quercus-Carya* (oak-hickory) forests using a stratified design to capture a variety of physiographic and edaphic conditions. Pre-harvest plot data were collected in 1988 and plots were resampled in 2011, allowing documentation of shifts in species composition over a 23-year period (1988–2011). Aerial photos from the 1930s were used to determine canopy cover and likely historic land-use within each stand prior to incorporation into the HNF. To characterize edaphic conditions, soil samples were collected and analyzed for chemical characteristics in 2011. Non-metric multi-dimensional scaling (NMS) and multiple linear regression using fixed and mixed-effect models were used to examine species composition along topo-edaphic and historic canopy cover gradients. We observed drastic declines in the importance of *Quercus alba* (white oak), *Quercus velutina* (black oak), and *Quercus prinus* (chestnut oak) across all stands following harvest. During the same time period, we observed large increases in the importance of other species, with *Acer rubrum* (red maple) showing large increases on the driest sites and *Liriodendron tulipifera* (tulip-poplar) displaying the greatest increase across all sites. In pre-harvest stands, *Q. prinus* was confined to the poorest sites and displayed the strongest association of all species with historically closed canopies in both pre and post-harvest stands. In post-harvest stands, the diminished importance of *Q. alba* was associated with low soil nitrogen levels and historically open canopies. *L. tulipifera* and *Prunus serotina* (black cherry) were associated with more nutrient-rich mesic sites in post-harvest stands. *Populus grandidentata* (big-tooth aspen) in post-harvest stands was associated with historically closed canopies and low cation exchange capacity.

1. Introduction

Quercus (oak) is an ecologically important genus in temperate forests throughout the world, with 32 overstory species in eastern North America, 21 in eastern Asia, 11 in Europe, and 5 in Pacific North America (Latham and Ricklefs, 1993). However, the sustainability of *Quercus* species across forest landscapes is threatened by climate-related mortality of mature trees (Jenkins and Pallardy, 1995; Demchik and Sharpe, 2000; Allen et al., 2010; Levanič et al., 2011), and wide-spread regeneration failure resulting from shifting disturbance regimes (Shrestha, 2003; Zavaleta et al., 2007; Plieninger et al., 2010; McEwan et al., 2011; Dey, 2014). Observed and predicted declines in *Quercus* species importance have caused great concern because significant reductions in oak abundance will likely have profound effects on forest

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ecosystems throughout the global range of the genus (Fei et al., 2011; Dey, 2014). *Quercus* is often considered a foundation genus because member species drive trophic interactions and influence population and community dynamics by providing hard mast and shelter for numerous vertebrate species (Ellison et al., 2005) and serving as habitat for large numbers of insect species (Opler, 1974; Futuyma and Gould, 1979; Vodka et al., 2009), often several times more than other co-occurring hardwood species (Southwood, 1961; Ranius and Jansson, 2000).

Many presettlement forests of eastern North American were pyrogenic as structure and composition was dependent on the recurrent use of fire by Native Americans (Nowacki and Abrams, 2008). During early Europeans settlement, fire frequencies increased and forests were cleared for row agriculture and livestock grazing, perpetuating disturbance-adapted *Quercus* species across the landscape (Guyette et al., 2005). In many eastern hardwood forests, the loss of *Castanea dentata* (American chestnut) also resulted in increased importance of *Quercus* species, particularly in the southern Appalachian Mountains (Nelson, 1955; Woods and Shanks, 1959). Starting in the early 20th century, fire suppression created drastic reductions in *Quercus* regeneration, especially on more productive sites (Dey, 2002). Although *Quercus* species remain dominant in the overstory of many forests, the lack of fire or surrogate disturbances have allowed them to be replaced by shade-tolerant and fire-sensitive species.

The desire to perpetuate *Quercus*-dominated forests fostered extensive research to identify silvicultural systems best suited to regenerating and sustaining the genus. In the eastern United States, even-aged reproduction systems in the form of clearcutting were deemed suitable and widely implemented throughout the range of *Quercus* species (McGee, 1987). Clearcut harvests were considered the most efficient and economically advantageous form of silviculture due to greater yields per hectare, lower harvesting costs, and simplified management (Clark and Watt, 1971; Sander and Clark, 1971). This technique was frequently viewed as a panacea for regenerating *Quercus* species and was implemented across much of the eastern United States from the 1960s through the 1980s (Roach and Gingrich, 1968; Sander and Clark, 1971).

Subsequent observations in post-harvest stands often found composition shifting away from *Quercus* domination towards a mix of hardwoods species, raising concerns about the efficacy of clearcutting (George, 1988). Early research in clearcuts suggested that site conditions determined the distribution and importance of *Quercus* species, with *Quercus* reproduction in greatest abundance on the poorest site, but rarely occurring on more productive sites where *L. tulipifera*, *Acer* spp., *P. serotina*, *Populus* spp., and *Fraxinus* spp. (ash species) dominated (Trimble and Hart, 1961; Hilt, 1985).

Understanding the post-harvest persistence of *Quercus* species requires a fine-scale examination of how the silvics of the genus interact with disturbance and environmental gradients. Several physiological and morphological characteristics give *Quercus* species an advantage under xeric conditions including the rapid development of a long taproot, the ability to photosynthesize and conduct water under high drought stress, and the maintenance of high root:shoot ratios through recurrent shoot dieback (Abrams, 1990; Pallardy and Rhoads, 1993; Parker and Dey, 2008; Johnson et al., 2009). However, these characteristics are associated with greater investment in belowground growth and may create a competitive disadvantage on more mesic sites with greater water availability.

The Central Hardwood Region (CHR) of the United States is the archetype of a region whose forests have experienced declines in *Quercus* species importance in response to shifting disturbance regimes. The Hoosier National Forest (HNF) in southern Indiana used clearcutting as its dominant harvesting prescription for approximately 20 years, ending in the late 1980s. As with much of the southern portion of the CHR, forests of HNF are underlain by bedrock (nonglaciated) substrate that creates gradients of moisture availability, microclimate, and soil fertility (Van Kley et al., 1995). Throughout the CHR, the forests that developed after clearcutting are now entering the understory re-initiation stage (Oliver and Larson, 1996), and more research is needed to understand how these forests developed across physiographic gradients as they enter later stages of stand development. In a chronosequence study of 9–27 year-old clearcuts, Jenkins and Parker (1998) found that clearcuts on mesic slopes contained greater importance of *L. tulipifera* than dry-mesic slopes where *Quercus* species competed better. While such chronosequence studies have provided valuable information, they may fail to capture ecological patterns and processes across environmental gradients that are better assessed by the resampling of long-term monitoring plots. Consequently, long-term datasets are critical to understanding forest development in post-harvest stands where a diverse array of overstory species and high inter-site variability may limit the use of a chronsequence (Walker et al., 2010).

In 1988, a long-term, repeated measure study was implemented on the HNF by the USDA Forest Service North-Central Experiment Station to examine the competitive ability of *Quercus* species after clearcutting and the post-harvest development of forest stands. In 2011, we resampled 55 plots that were established prior to harvesting in 1988 and used these data to examine the importance of *Quercus* species and their competitors in pre- and post-harvest stands. We also examined how species were distributed across gradients created by historical land use and topo-edaphic characteristics. Based upon these examinations, we address three primary questions:

1. How do the distributions of species differ between pre- and post-harvest stands in relation to underlying environmental gradients?
2. How have land-use practices prior to the creation of the HNF (represented by canopy cover in 1938–1940 aerial photos) influenced the pre- and post-harvest composition of sampled stands?
3. Where across contemporary environmental and disturbance gradients are *Quercus* species best able to persist in post-harvest stands?

2. Methods

2.1. Harvest treatments

In 1988, six mature *Quercus-Carya* dominated stands ranging in size from 4.5 to 12.1 ha were harvested on the HNF. Three of the stands were located on the Brownstown Ranger District and three stands were located on the Tell City Ranger District (Table 1). All stands were clearcut for merchantable timber between the months of April and August 1988. After removal of merchantable timber, all remaining live and cull trees ≥ 5.1 cm dbh (diameter at breast height) were felled. No herbicide treatments or additional site preparation treatments were performed.

2.2. Study sites

Stand 1 is located in the Brown County Hills Section of the Highland Rim Natural Region (Homoya et al., 1985). This section is characterized by deeply dissected uplands underlain by siltstone, sandstone, and shale. Soils are Brownstone channery silt loams, which are moderately deep and well drained soils formed in residuum from siltstone. Steep slopes and narrow hollows are typical topographic features of this section (Van Kley et al., 1995). There is little disparity in forest composition, with *Quercus-Carya* dominated uplands often consisting of nearly pure stands of *Q. prinus* on upper slopes and ridge tops. Mesic ravines harbor species such as *Fagus grandifolia* (American beech), *Quercus rubra* (northern red oak), *Acer saccharum* (sugar maple), and *Fraxinus americana* (white ash).

Stands 2, 3, and 6 are located in the Crawford Upland Section of the Shawnee Hills Natural Region (Homoya et al., 1985). The broad ridge tops and flats of this section contrast with the narrow ridges and steep terrain of the Brown County Hills Section. Stand 2 is underlain by Wellston-Tipsaw-Adyeville Complex (Ultic Hapludalfs, Typic