



Fear, fire, and behaviorally mediated trophic cascades in a frequently burned savanna



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ABSTRACT

Ecologists increasingly recognize the importance of trait-mediated indirect interactions and suggest behavioral traits aimed to reduce predation risk can induce trophic cascades. However, the application of theory developed in simple experimental systems to complex natural systems has spurred debate regarding whether predation risk, independent of direct killing, can structure ecosystems. We examined the effects of white-tailed deer (*Odocoileus virginianus*) foraging under the risk of predation by coyotes on oak (*Quercus* spp.) regeneration and the abundance of palatable understory species in a frequently burned longleaf pine savanna. Oaks represent a common but relatively low quality forage item for deer, and are an important component of this system because oak encroachment into pine-dominated uplands can reduce biodiversity. In frequently burned ecosystems oaks and other fire-impeding species often exist in a demographic fire-trap, where they sprout following fire but rarely escape into the midstory, because they are repeatedly top-killed by subsequent fires. Many factors including herbivory stress can influence the probability of fire survival for oak saplings. Other Cervids, including elk (*Cervus canadensis*) and moose (*Alces alces*) are known to increase use of woody browse with predation risk because of selection for brushy areas that offer concealment cover. We experimentally manipulated predation risk for 10 years, by establishing 4 approximately 40-ha predator exclosures and 4 control plots to test the effects of predation risk on aspects of the plant community. Reduced predation risk resulted in increased oak recruitment and decreased abundance of palatable forage. A density-mediated trophic cascade does not explain the release of oaks and our results provide support for the behaviorally-mediated trophic cascade hypothesis. We offer evidence that frequent disturbance can facilitate trophic cascades and that predator-sensitive foraging can enhance fire suppression of oaks and influence groundcover composition in longleaf pine savannas.

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1. Introduction

Recent evidence suggests predators can exert powerful top-down effects on ecosystems by influencing prey abundance and behavior (Myers et al., 2007; Estes et al., 2011; Ripple et al., 2014). Trophic cascades explain interactions between predators, and the resources their prey consume (Paine, 1980), and often arise when predators protect plants by reducing herbivore abundance. Behaviorally mediated trophic cascades (BMTCs) can occur when predators alter foraging behavior of herbivores (Beckerman et al., 1997; Schmitz et al., 2004). Experimental evidence of BMTCs is abundant, but has largely been restricted to invertebrates or

aquatic systems, leaving some to question the strength or existence of BMTCs in complex terrestrial systems involving large vertebrate predators (Halaj and Wise, 2001; Shurin et al., 2002; Kauffman et al., 2010; Winnie, 2012). Yet, the BMTCs hypothesis is appealing given the abundance of evidence demonstrating predators can affect when, where, how, and on what herbivores feed (Lima and Dill, 1990). Prey species often respond to predation risk by retreating to safer habitats (Werner et al., 1983), increasing vigilance while foraging (Cherry et al., 2015), and altering diet selection (Beckerman et al., 1997; Banks et al., 1999) all of which can influence herbivory.

Longleaf pine-wiregrass (*Pinus palustris*–*Aristida stricta*) savannas of the southeastern USA are characterized by globally significant levels of biodiversity, with numerous endemic flora and fauna species (Mitchell et al., 2006). A frequent, (e.g. 1–3 years) fire-return interval maintains a sparse canopy and limits midstory

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encroachment by fire-impeding species such as oaks (*Quercus* spp.; Glitzenstein et al., 1995; Kirkman et al., 2004). Canopy species are considered “pyro-engineers” contributing litter of varying flammability to the fuel bed beneath their crowns (Kane et al., 2008; Ellair and Platt, 2013; Fig. 1). Longleaf pine litter is more flammable than the litter of most hardwoods, and canopy heterogeneity can cause fine-scale variation in fire severity that can influence aboveground damage and survival of understory plants, germination of legumes and grasses, and future forest conditions (Williamson and Black, 1981; Thaxton and Platt, 2006; Ellair and Platt, 2013; Wiggers et al., 2013). Many fire-impeding tree species exist in a “fire trap,” or demographic bottleneck where they repeatedly sprout after loss of aboveground biomass, but rarely escape into larger size classes (Grady and Hoffmann, 2012). When fire-impeding hardwoods escape the fire trap, the midstory closes, their influence as pyro-engineers increases with crown size resulting in less frequent and more severe fires (Mitchell et al., 2006; Grady and Hoffmann, 2012). Oak encroachment into the midstory of longleaf pine woodlands adversely affects threatened and endangered species including the red-cockaded woodpecker (*Picoides borealis*) and gopher tortoise (*Gopherus polyphemus*), and decreases plant diversity (Walters, 1991; Kirkman et al., 2004; Mitchell et al., 2006).

Fire and herbivory can interact to influence the balance of trees and grasses in savanna systems (Scholes and Archer, 1997; Higgins et al., 2000; Barnes, 2001; Sankaran et al., 2004). For example, Staver et al. (2009) demonstrated that both fire and browsing reduced tree growth, but only their combined effects limited tree density in an African savanna. Aboveground fire survival of oaks in frequently burned longleaf pine savannas is a function of size of the oak at the time of fire, local fuel characteristics, and fire conditions (Glitzenstein et al., 1995; Ellair and Platt, 2013). Growth of oak saplings following fire can be affected by herbivory (Adams and Rieske, 2001), and thus foraging behavior and abundance of herbivores could influence fire survival of oak sprouts and ultimately the selectivity of the fire trap and future forest conditions.

In the southeastern USA, coyotes (*Canis latrans*) have been linked to declines in white-tailed deer (*Odocoileus virginianus*; hereafter deer) fawn survival (Kilgo et al., 2012; Nelson et al., 2015), recruitment (Gulsby et al., 2015), and population growth (Kilgo et al., 2010). In spite of potentially overestimating survival due to capturing fawns at 3–4 days of life (Gilbert et al., 2014), on our study site, the Joseph W. Jones Ecological Research Center at Ichauway in southwestern Georgia, fawn survival probability to 20 weeks was only 29% (Nelson et al., 2015). Following an experimental predator removal, fawn–adult female ratios, an index of recruitment, increased by approximately 150%, suggesting recruitment may be predator limited in our system (Howze et al., 2009). Coyote predation risk also induces both proactive (Conner et al., 2016) and reactive (Cherry et al., 2015) behavioral responses during the fawn-rearing season on our site. Conner et al. (2016)

documented that white-tailed deer use of predator exclosures (i.e., 4, 40 ha fenced pens permeable to deer but excluding coyotes) was approximately 5 times greater than control plots during a 10 year study. Cherry et al. (2015) demonstrated that adult female white-tailed deer decreased vigilance while foraging at baited camera traps in predator exclosures relative to control plots. Collectively these studies suggest adult female white-tailed deer face high predation on their offspring and respond with a suite of antipredator defenses.

Deer are the largest herbivore in the longleaf pine ecosystem, consume browse of many fire-impeding species (e.g., oaks), potentially decreasing sprout or sapling fire survival, and have the ability to strongly influence forested ecosystems through herbivory (Cote et al., 2004). Cervids, including elk (*Cervus Canadensis*; Creel and Christianson, 2009) and moose (*Alces alces*; Edwards, 1983) are known to increase use of woody browse with predation risk because of selection for brushy areas that offer concealment cover. For example, in the presence of wolves (*Canis lupus*), elk increased use of forested cover (Creel et al., 2005), decreased grazing and increased browsing (Christianson and Creel, 2008), and increased consumption of willow (*Salix* spp.; Creel and Christianson, 2009). Like other cervids, deer likely increase use of woody browse with increased predation risk because they often seek refuge in thick cover when faced with predation risk (Grovenburg et al., 2012). On our site female deer selected for areas with greater time-since-fire during the pulse of risk associated with fawning, in spite of forage in recent burns being of higher nutritional content and digestibility (Cherry et al., Submitted for publication). This counterintuitive avoidance of recently burned patches was explained by predation risk. Cherry et al. (Submitted for publication) documented that deer vigilance while foraging decreased with increasing time-since-fire suggesting that unburned patches are perceived by deer as safer than the surrounding savanna. Therefore, we predicted that deer would increase use of oaks in longleaf pine savannas under high predation risk because (1) oaks are often associated with concealment cover provided by unburned patches (i.e., thickets of Harcombe et al., 1993; oak domes of Guerin, 1993); (2) oaks presumably require a less search time due to greater height than most other forage options in biannually burned woodlands; (3) saplings can be browsed while maintaining a vigilant posture. Oak browse is common forage for deer in longleaf pine savannas, but is of relatively low quality (Lashley et al., 2015). In contrast, we predicted that the density of high-quality selected deer forage species would be higher in risky areas due to predation risk reducing herbivory (Callan et al., 2013; Waser et al., 2014). We hypothesized that deer would be highly interactive with adjacent trophic levels in longleaf pine ecosystem because of the potential for their herbivory to influence fire-mediated demographic bottlenecks of species considered pyro-engineers; and coyote predation can influence deer abundance and foraging behavior (Kilgo et al., 2010;



Fig. 1. The left panel is an illustration of “pyro-engineering” of fire-impeding species in a longleaf pine savanna and demonstrates how variation in fire severity can influence forest structure. The time since fire in this unburned patch will be two years greater than the surrounding stand. The right panel is an illustration of the interface between a pine savanna and an unburned patch that has escaped several fire cycles. Note the top-killed hardwoods stems in the foreground. The expansion and contraction of these unburned patches is driven by the fire survival of fire impeding species on the perimeter of the patches.

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