Effects of fire on acorn removal and deer mediated community level indirect effects of mast seeding

Charles Moriah Boggess

Follow this and additional works at: https://scholarsjunction.msstate.edu/td

Recommended Citation
Boggess, Charles Moriah, "Effects of fire on acorn removal and deer mediated community level indirect effects of mast seeding" (2020). Theses and Dissertations. 1744.
https://scholarsjunction.msstate.edu/td/1744

This Graduate Thesis - Open Access is brought to you for free and open access by the Theses and Dissertations at Scholars Junction. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of Scholars Junction. For more information, please contact scholcomm@msstate.libanswers.com.
Effects of fire on acorn removal and deer mediated community level indirect effects of mast seeding

By

Charles Moriah Boggess

Approved by:

Bronson K. Strickland (Major Professor)
Marcus A. Lashley
Heather D. Alexander
Kevin M. Hunt (Graduate Coordinator)
George M. Hopper (Dean, College of Forest Resources)

A Thesis
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Master of Science
in Wildlife, Fisheries, and Aquaculture
in the Department of Wildlife, Fisheries, and Aquaculture

Mississippi State, Mississippi

August 2020
Copyright by

Charles Moriah Boggess

2020
Declining oak (Quercus spp.) dominance across the eastern U.S. is often attributed to fire exclusion and abundant white-tailed deer (Odocoileus virginianus). Fire restoration can negatively affect acorn germination and survival directly but also indirectly through impacts on seed predation. Similarly, masting events could influence oak regeneration success by altering deer behavior. To date, virtually no information exists assessing indirect effects of acorn consumers on oak regeneration. I developed two experiments to address this knowledge gap. In the first experiment, I determined if burning acorns affects predator removal rates. In the second experiment, I assessed the indirect effects of mast seeding on plant communities mediated by deer. Burning acorns decreased acorn removal rates. This could increase survival to spring for acorns that survived exposure to fire. Mast seeding increased local deer use, decreased the competitive advantage of local oak seedlings, but increased beta diversity in the understory.
DEDICATION

This thesis is dedicated to my English and science teachers during my first eight years of homeschool education, namely my mom and dad. Their selfless dedication, sacrifice, and determination to provide me a good education prepared me for my college studies. Their love of the outdoors and incredible work ethics were inspirational to me from a young age, giving me a passion for the outdoors and determination to work hard. My mom’s tireless work to teach me proper communication skills while I was young gave me an appreciation for grammar and writing skills that have proven invaluable to my education. My dad’s creativity and optimism have taught me not to limit my dreams but instead embrace creativity and shoot for the stars. I would not be the person I am today without my parents’ support and selflessness.
ACKNOWLEDGEMENTS

First, I would like to thank all of my family and friends who have supported me through my education. A huge thank you to my major advisor Dr. Marcus Lashley for providing me an awesome graduate school opportunity. I have learned much from him, and his excitement for ecology has inspired my own interests in conservation on a broader level. Thanks to Dr. Bronson Strickland for his willingness to take over as my advisor when circumstances changed. You have been a great role model, showing me how to communicate science to others. Also, thank you to Dr. Heather Alexander for giving me research support and adopting me into the Forest and Fire Ecology Lab.

I could not have completed my research without the generosity and tremendous hospitality of Bob and Sheryl Bowen who provided me a wonderful study area, field house, and some of the best home cooked meals in the South, thank you both! Thanks to Stephanie Green and the Strawberry Plains Audubon Center for their generosity in providing an additional study area. Thanks to the MSU Department of Wildlife, Fisheries, and Aquaculture for funding my project and all my fellow graduate students for providing an exceptional work environment.

Finally, I would like to specifically thank Dr. Carolina Baruzzi, David Mason, Adrienne Dykstra, Giancarlo Coppola, Luke Resop, Corianne Schmidt, Brandon Taylor, and all of my fellow Deer Lab and Fire Ecology Lab students who have volunteered their time and expertise to my research. These projects would not have been possible without anyone mentioned above, thanks to all!
# TABLE OF CONTENTS

DEDICATION ........................................................................................................................................ ii

ACKNOWLEDGEMENTS .................................................................................................................... iii

LIST OF TABLES .................................................................................................................................... vi

LIST OF FIGURES ............................................................................................................................... vii

CHAPTER

I. INTRODUCTION ............................................................................................................................... 1

   Literature Cited ................................................................................................................................... 4

II. EXPOSURE TO FIRE REDUCES HAZARD OF ACORNS TO REMOVAL BY CONSUMERS ............... 8

   Introduction .......................................................................................................................................... 8

   Materials and Methods ....................................................................................................................... 11

      Study Areas ...................................................................................................................................... 11

      Acorn Treatments .............................................................................................................................. 12

      Data Collection ................................................................................................................................. 14

      Data analysis ..................................................................................................................................... 15

   Results ................................................................................................................................................ 16

   Discussion ............................................................................................................................................ 18

   Conclusions ......................................................................................................................................... 21

   Literature Cited ................................................................................................................................... 24

III. FACULTATIVE SEED PREDATORS DRIVE COMMUNITY-LEVEL INDIRECT EFFECTS OF MAST SEEDING 30

   Introduction .......................................................................................................................................... 30

   Materials and Methods ....................................................................................................................... 33

      Study Site ......................................................................................................................................... 33

      Experimental Design ......................................................................................................................... 34

      Data Collection .................................................................................................................................. 36

      Data Analysis .................................................................................................................................... 36

   Results ................................................................................................................................................ 37

   Discussion ............................................................................................................................................ 39
Management Implications ........................................................................................................................................... 42
Literature Cited .......................................................................................................................................................... 47

APPENDIX

A. SUPPLEMENTAL RESULTS OF PAIRWISE COMPARISONS FOR SIGNIFICANT INTERACTION TERMS WITHIN COX MIXED REGRESSION MODELS ........................................................................................................................................... 53
LIST OF TABLES

Table A.1  Pairwise comparisons of acorn species removal probabilities from highest ranked model without (= 0) and with (= 1) caching predator presence..........................55

Table A.2  Coefficient estimates from second highest ranked model........................................59
LIST OF FIGURES

Figure 2.1 Coefficients for highest ranked Cox mixed regression model ........................................22
Figure 2.2 Persistence probability of acorns in treatment plots ...................................................23
Figure 3.1 Acorn addition experimental plot design .................................................................44
Figure 3.2 Conceptual deer use, deer feeding detections, conceptual plant cover, and species accumulation by treatment and among acorn addition treatments ..........45
Figure 3.3 Difference in relative growth stem length between Shumard oak and blackgum seedlings ..............................................................................................................46
Figure A.1 Pairwise comparisons between acorn species from highest ranked model ..........54
Figure A.2 Coefficients for second highest ranked Cox mixed regression model .............58
Oaks (*Quercus* spp.) historically dominated upland savannahs, woodlands, and forests of the eastern U.S., but are now declining in dominance (Abrams 1992, Fei et al. 2011). Oaks have increased in volume in recent years but have concurrently decreased in density and percent cover (Fei et al. 2011, Moser et al. 2006). These changes in oak population dynamics have been driven by maturing oak stands and a lack of successful regeneration to replace adult trees (Fei et al. 2011, McWilliams et al. 2002). Seedling densities, while remaining abundant, are not advancing into larger size classes and are accumulating in the understory (Abrams 1992, Moser et al. 2006). This bottleneck in the seedling bank has resulted in a regeneration gap in sapling and midstory oaks compared to other size classes (Aldrich et al. 2005, McShea et al. 2007, Moser et al. 2006, Spetich et al. 2011). The bottleneck in oak regeneration has been attributed in part to two factors: 1) fire exclusion (Abrams 1992, Albrecht and McCarthy 2006), and 2) high contemporary white-tailed deer (*Odocoileus virginianus*) density (Marquis and Brenneman 1981, McShea et al. 2007). Although climate change, land use changes, loss of American chestnut and passenger pigeons also may be contributing factors (Hanberry et al. 2020, McEwan et al. 2011).

Fire is an essential natural disturbance that may facilitate oak regeneration by decreasing competition from fire-sensitive, shade-tolerant species through top-killing of seedlings and increasing light availability (Clark 1993, Nowacki and Abrams 2008). However, fire has been intentionally excluded in oak systems since the turn of the 20th century, and only over the past 50
years has prescribed fire been gradually returned to some managed forests (Abrams 1992, Fowler and Konopik 2007, Nowacki and Abrams 2008, Spetich et al. 2011). Prescribed fire is most often conducted in late winter to early spring, but limited days with appropriate fire weather conditions during this burn window often limits how much acreage is burned (Knapp et al. 2009, Ryan et al. 2009). Fall burns could help to extend the burn window because there is a high proportion of good fire weather days in fall that are often underutilized by managers (Chiodi et al. 2018). Because fall prescribed fire negatively affects acorn germination of freshly fallen acorns, some scientists have made recommendations discouraging fall burning during good seed crops (Auchmoody and Smith 1993, Cain and Shelton 1998, Greenberg et al. 2012, Nation et al. 2020). However, many acorns survive low to moderate intensity surface fires and others are cached by seed predators prior to fire, protecting them from exposure (Auchmoody and Smith 1993, Cain and Shelton 1998, Greenberg et al. 2012, Greenler 2020, Nation et al. 2020, Thorn and Tzilkowski 1991). The effect of seed predator removal on acorns is heavily dependent on whether predators removing seeds are seed cachers or not, affecting whether seeds are immediately consumed or are cached with some chance to survive and germinate (Haas and Heske 2005, McShea and Schwede 1993, Smith and Reichman 1984, Steiner 1996, Vander Wall 1990). Fire can have a dramatic effect on habitat quality and behavior of wildlife in oak forests and may change which and how heavily various species rely on acorns as a food source (Harper et al. 2016). Thus, acorn removal by predators could complicate the net effects of fall fire on acorn success if burning alters consumer preference for acorns or if the rate at which acorns are depredated or cached changes with fire.

Deer selectively eat leaves and stems of a wide range of plant species in the understory (Bryant et al. 1979, Crawford 1982, Jones et al. 2008, Lashley et al 2011, Lashley et al. 2016, ...
Meyer et al. 1984, Reynolds et al. 1992). Selective herbivory by deer can affect the trajectory of plant communities and may mediate competition between plants (DeCalesta 1997, Horsley and Marquis 1983, Jordan 1967, Stromayer and Warren 1997). Deer are also one of the most important vertebrate acorn predators, with fall diets comprised mostly of acorns during mast years (Harlow et al. 1975, McCullough 1985, McShea and Schwede 1993, Steiner 1996). Unlike obligate acorn predators, deer populations are relatively independent of mast cycles making them less susceptible to predator satiation and a formidable predator of acorns (Harlow et al. 1975). Because of the attractiveness and relative importance of acorns to deer, oaks may concentrate deer use under their crowns during mast years effectively linking masting indirectly to the established understory plant community. Thus, oak masting events could indirectly change competition between oak and non-oaks seedlings and the structure of the local plant community.

I designed two manipulative experiments to examine 1) indirect effects of fall fire on acorn removal and 2) community-level indirect effects of oak masting. In Chapter II, I assessed effects of fall fire on removal rates of acorns using cafeteria style plots with burned and unburned acorns of eight oak species. I used Cox proportional hazard models to test for effects of fire, predator functional group, and acorn species on relative hazard of acorns. In Chapter III, I examined effects of mast seeding on local deer use, acorn survival, relative competition of oak seedlings with a competitor, and species richness by simulating mast seeding via acorn additions. These experiments provide important information on the role of species interactions in oak regeneration dynamics.
Literature Cited


CHAPTER II
EXPOSURE TO FIRE REDUCES HAZARD OF ACORNS TO REMOVAL BY CONSUMERS

Introduction
Poor regeneration across much of the eastern U.S. is causing oaks (*Quercus* spp.) to decrease in relative density compared to other hardwood species (Abrams 1992, Fei et al. 2011). Failure of oak regeneration has been attributed to seedlings accumulating in the understory stratum and not advancing into the midstory causing a regeneration bottleneck (Abrams 1992, Aldrich et al. 2005, McShea et al. 2007, Moser et al. 2006). There are many hypothesized explanations for observed changes in oak demographics such as the loss of American chestnut, climate change, changing land uses, and deer herbivory, but the fire-oak hypothesis has been the most widely accepted and tested explanation for oak declines, positing that intentional fire exclusion is favoring fire-sensitive and fast-growing non-oak hardwoods (Abrams 1992, Albrecht and McCarthy 2006, Hanberry et al. 2020, McEwan et al. 2011, Nowacki and Abrams 2008). Prescribed fire alone or in combination with canopy reductions has been promoted as a tool to improve oak regeneration (Albrecht and McCarthy 2006, Arthur et al. 2012, Brose et al. 2013, Brose 2014, Nowacki and Abrams 2008), but seasonally constrained burn windows often limit application (Chiodi et al. 2018, Haines et al. 2001, Kobziar et al. 2015).

Fall is likely a prime season to expand the prescribed burn window in the eastern US because of the high proportion of acceptable burn days in this season with relatively low
utilization by managers (Chiodi et al. 2018). Perceived negative effects of fall prescribed fire on freshly fallen acorns has raised concern and lead to some studies measuring effects of fall fire on acorn germination and seedling establishment (Auchmoody and Smith 1993; Cain and Shelton 1998; Greenberg et al. 2012; Greenler et al. 2019, 2020; Nation et al. 2020). Management recommendations generated from many of these studies discourage the use of fall prescribed fire after acorn drop because of the reduction in germination rates of acorns, but cached seeds and seeds not killed in burned stands may perform as well or better than acorns in unburned stands (Auchmoody and Smith 1993, Greenberg et al. 2012, Greenler et al. 2020). Fire strongly influences wildlife habitat quality for many species of acorn consumers and in doing so, affects their behavior and abundance (Harper et al. 2016). For example, fire affects selection of burned patches by seed predators and may affect acorn success by altering removal rates. The magnet effect has been described across many systems where large herbivores respond positively to patches recently burned (Allred et al. 2011, Archibald et al. 2005, Klop et al. 2007, Pearson et al. 1995, Westlake et al. 2020). This magnet effect on large seed predators who do not cache seeds likely reduces acorn viability via increased removal of acorns. An opposite effect on small mammals selecting against areas with reduced cover following fire may decrease removal by these caching seed predators (Greenler et al. 2019, Kennedy and Peter 2005, Pérez-Ramos and Marañón 2008). However, other indirect fire effects such as shifting preference for acorns by seed predators have not yet been assessed.

Removal of acorns by seed predators often has negative effects on acorn success, but the outcome of these removals is heavily dependent on whether the predator is a seed cacher or not. Caching consumers can have important effects on the likelihood of germination and seedling establishment based on the choice to consume or cache acorns (Haas and Heske 2005, McShea
and Schwede 1993, Smith and Reichman 1984, Steiner 1996, Vander Wall 1990). Caching predators consume most acorns they cache, but those left in caches (Cahalane 1942, Steele et al. 2001) typically have a higher survival rate and better seedling establishment success than acorns on the surface (Borchert et al. 1989, Fuchs et al. 2000, Greenler et al. 2020, Griffin 1971, Nyandiga and McPherson 1992, Vander Wall 2001). However, not all seed predators cache acorns. Many seed predators only consume acorns they remove, rendering them nonviable. Therefore, it is better for an acorn to be removed by a caching predator and possibly deposited in a suitable germination site than to have no chance of survival when being removed by a non-caching predator.

Fire may indirectly affect acorn viability by altering the relative removal rates by caching and non-caching predators through direct effects on acorn palatability. Cooking via heat is a food preparation method heavily employed by humans and an important tool used for rendering acorns palatable for consumption (Bainbridge 2006, Mason 1995, Wrangham 2009). There is also strong evidence that fire influences wildlife food preferences (Harper et al. 2016) and fire is even used as a tool in foraging (Foster et al. 2020). It seems reasonable that heating of acorns through prescribed fire may change palatability in ways that influence preference and removal rates of wildlife. Caching seed predators can detect acorn soundness and choose whether to cache or consume acorns based on viability (Muñoz and Bonal 2008, Steele et al. 1996). Since fire affects the soundness of acorns (Auchmoody and Smith 1993, Cain and Shelton 1998, Greenberg et al. 2012, Greenler et al. 2020, Nation et al. 2020) this could indirectly affect acorn fate by changing predator choice, and if this effect differs between caching and non-caching seed predators, it could further influence fire effects on acorn success. Moreover, this effect may vary by oak species which likely differ in their relative tolerance to fire exposure. Historically, upland
sites experienced more frequent fire than did bottomlands (Frost 1998) which may have promoted fire tolerant traits in acorns of upland species. If fire adaptations change the resistance of acorns to direct fire effects, and acorn soundness affects selection, there may be differential effects of fire on acorn removal rates across species of oaks.

To date, little data exist to assess the potential indirect effects of fire on acorn viability mediated through seed predator removals. Therefore, I designed a replicated cafeteria style experiment using unburned and burned acorns of eight oak species to determine whether direct exposure of acorns to fire could indirectly affect acorn viability as mediated by interactions with consumers. I used camera traps monitoring acorn removal by wildlife to test the predictions that fire would decrease removal rates of acorns differently across oak species and alter the relative removal of acorns by caching and non-caching predators. These results will provide important baseline information to understand the potential for exposure of acorns to fire indirectly affecting acorn viability.

**Materials and Methods**

**Study Areas**

Cafeteria-style acorn plots were deployed at Spirit Hill Farm (SHF; 492 ha) and Strawberry Plains Audubon Sanctuary (STP; 1016 ha), located 26 km apart in NW Mississippi, USA, 7.5 km N and 25 km WSW of the city of Holly Springs, respectively. Plots were placed in temperate mixed upland hardwood stands on both sites. The dominant overstory in both stands included white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Münchh.), southern red oak (*Q. falcata* Michx.), post oak (*Q. stellata* Wangenh.), sweetgum (*Liquidambar styraciflua* L.), and mockernut hickory (*Carya tomentosa* (Poir.) Nutt.). The non-
oak midstory hardwood component was dominated by sweetgum, blackgum (Nyssa sylvatica Marshall), red maple (Acer rubrum L.), and winged elm (Ulmus alata Michx.). Understory vegetation was sparse across all plot sites and dominated by deerberry (Vaccinium stamineum L.) and seedlings of trees found in the midstory and overstory.

**Acorn Treatments**

To test fire effects on acorn removal across oak species with varying levels of fire adaptations, acorns from four upland and four bottomland oak species occurring in the southeastern U.S. were used for my study. Shumard oak (Q. shumardii Buckley), cherrybark oak (Q. pagoda Raf.), willow oak (Q. phellos Michx.), and Nuttall oak (Q. texana Buckley) acorns were collected below trees in Starkville, MS, USA during November and December 2019. Southern red oak, northern red oak (Q. rubra L.), black oak, and scarlet oak were purchased from Louisiana Forest Seed Company, Lecompte, LA. All acorns were visually inspected for viability (Morina et al. 2017) and non-viable acorns were discarded. Acorns were stored inside plastic bags in refrigerated storage at 4 °C until use. I only used species from the red oak group (Erythroxylum subgenus) for my experiment because species from the white oak group (Leucobalanus subgenus) germinated in refrigeration within days of collection.

Five 1-m² plots were established in a bare mineral soil opening on Andrews Forestry & Wildlife Laboratory near Starkville, MS, USA with no vegetation or other fuels present. Leaf litter consisting of post oak, white oak, and southern red oak was collected from an upland hardwood stand at SHF and dried indoors for 2 weeks prior to burns. I added 360 g/m² (air dry weight) of oak leaf litter to each plot to replicate average fine fuel loads during fall at SHF (Nation et al. 2020). Leaf litter was left to acclimate to ambient temperature and moisture in burn
plots overnight. Eight 20 x 40-cm subplots were outlined within burn plots using a string grid, and acorn species were randomly assigned a subplot in every burn plot. Thirty acorns of each species were evenly distributed in their respective subplots and gently shaken into the top of the leaf litter to match acorn densities typical of excellent mast crops and location in leaf litter stratum typical during fall fire (Lashley et al. 2009, Greenberg et al. 2012, Brooke et al. 2019). All acorn species were burned in each fire plot so that heterogeneity in fire intensity would be distributed across species of acorns and reduce likelihood that one species experienced more intense fire than others.

To relate fire temperature in my experimental burns to those conducted in other studies, five pyrometers were placed at the leaf litter surface in each burn. Pyrometers were constructed of aluminum tags painted with six Tempilaq® fire-sensitive paints (Tempil, South Plainfield, New Jersey, USA) that melt and change color at specific temperatures (79, 163, 246, 316, 399, and 510 ºC (Arthur et al. 2015), ambient air temperature was used for pyrometers having no paint melt. Fuel consumption was estimated visually, and litter depth was measured as the difference between pyrometers and the soil surface following fires.

Burns were conducted between 1100 and 1230 on January 22, 2020 when air temperature was 6 - 9.7 ºC, relative humidity was 28.5 – 39.6 %, and winds were out of the west at 1 - 2.5 m/s (Kestrel® 5500 Fire Weather Pro, Boothwyn, PA, USA). Ring fires were lit in a leaf litter ignition zone 10 cm outside the perimeter of plots with a drip torch using a 3:1 mixture of diesel fuel and gasoline. Fire rate of spread was (61 ± 27 s), measured as time passed between when fire entered the plot to when it reached plot center. Maximum flame height (27 ± 3 cm) was visually estimated during each burn by continually comparing flame height to a metal meter stick.
placed on the opposite side of the plot from the observer. Mean maximum fire temperature was 257 ± 17 °C, mean litter depth was 4.7 ± 0.4 cm, and mean fuel consumption was 94.4 ± 0.7 %.

My measurements of fire characteristics were comparable to those from other acorn fire experiments in upland oak systems (Greenberg et al. 2012, Nation et al. 2020). After burns, acorns were collected from their respective subplots and aggregated in plastic bags by species and placed in refrigeration at 4 °C until acorn removal plots were established.

**Data Collection**

To measure acorn removal rates, 10 plot locations (≥ 500 m apart) were selected in upland hardwood stands with similar understory communities on both study sites. On each study site five plots were randomly assigned the burned acorn treatment, and the other five were assigned the unburned acorn treatment. Each plot consisted of nine white circular trays with diameters of 17.7 cm and depths of 2 cm. Tray bottoms were covered with 1 cm of white play sand (QUIKRETE®, Atlanta, GA) and placed in a 3 X 3 grid pattern with a ≈15 cm gap between rows and columns of trays. Each species was randomly assigned a tray and 10 acorns from the respective species were spread across the sand surface. One tray in each plot did not receive acorns. I monitored acorn removal using Bushnell Trophy Cam infrared camera traps set on a 1-minute delay, 30 second video, and “normal” PIR sensor mode. Cameras were placed 3.5 m above the ground on an adjacent tree facing down over the top of plots. Additionally, cameras were set to take a video hourly so a count of acorns could be taken in case predators did not trigger cameras during removal. Plots were deployed on Jan. 24th and 25th and ran until Feb 11th; they were visited weekly to check camera and acorn status.
I reviewed each video and recorded metadata, the number of predator species visits, and the number of acorn removal events. These data were then transformed so that every acorn’s status was recorded every day it persisted in a plot leading up to an event (0 = persisting in plot, 1 = removed). Seed predators were grouped by functional group with the following grouped as caching predators: southern flying squirrel (*Glaucomys volans* L.), gray squirrel (*Sciurus carolinensis* Gmelin), fox squirrel (*Sciurus niger* L.), mice (*Peromyscus* spp.), vole (*Microtus* spp.). Non-caching predators included raccoon (*Procyon lotor* L.), white-tailed deer (*Odocoileus virginianus* Zimmerman), wild turkey (*Meleagris gallopavo* L.), and Virginia opossum (*Didelphis virginiana* Kerr).

In one predator removal plot, an acorn tray only received nine acorns due to miscounting during plot setup. In another plot, three trays were not visible to the camera trap following setup. The camera trap on this plot was moved by a fox squirrel two days after deployment so that the plot could not be observed. Thus, we excluded unobserved acorns from the dataset and concluded the experiment for all acorns surviving in the plot when they were no longer visible following the interference.

**Data analysis**

All analyses were performed in R (R Core Team 2019) and significance levels were set at 0.05. I used time dependent Cox mixed regression models (coxme package; Therneau 2020) to test the effect of variables on the probability that acorns would be removed from plots over time. Because 15 cameras did not auto-trigger every hour but once a day, I used daily persistence of acorns in plots as my time response value. I used the following independent variables: 1) acorn burn treatment (i.e., unburned or burned), 2) non-caching predator visits 3) caching predator
visits, 4) acorn species, 5) interaction between acorn treatment and non-caching predator visits, 6) interaction between acorn treatment and caching predator visits, 7) interaction between acorn treatment and acorn species, 8) interaction between acorn species and non-caching predator visits, 9) interaction between acorn species and caching predator visits, and 10) study site. Non-caching predator visits and caching predator visits were binomial time dependent variables, so I recorded every day if predators were recorded visiting my plots, and I used plot as a random effect term within all models. Due to the high number of independent variables, I adopted a model selection approach to test all possible combinations of independent variables and rank models based on their Akaike Information Criterion (AIC) (Akaike 1974). Models within 2 ΔAIC of the top ranked model were considered to have substantial support (Symonds and Moussalli 2011). Pairwise comparisons for the competing models were tested with the Tukey’s honest-significance-difference test (multicomp package; Hothorn et al. 2008). Hazard ratios from exponential coefficients in the model output were used as a relative index for comparing changes in probability of acorn removal (Anderson 1983).

**Results**

Mean acorn predator removal plot run time was 12.75 days with a range of 2-18 days before plots were terminated, determined by the length of time necessary for all acorns to be removed or when no acorns had been removed for several days. Of 1,579 acorns observed across plots, 1,540 were removed before the end of the study.

The top ranked model included the following independent variables: treatment interaction with non-caching predator presence, treatment interaction with caching predator presence, and an acorn species interaction with caching predator presence. Treatment had a significant effect on removal probability (Coeff. = 2.817, \( p < 0.01 \)), reducing removal probability for burned acorns
There were significant treatment interactions with both caching (Coeff. = -0.845, p < 0.01) and non-caching seed predators (Coeff. = -1.906, p < 0.01) that both reduced the treatment effect (Figure 2.1). The second highest ranked model was within 1 AIC point of the first and included the following independent variables: treatment interaction with non-caching predator presence, treatment interaction with caching predator presence, an acorn species interaction with caching predator presence, and study site (Table A.2 and Figure A.2).

In species pairwise comparisons southern red and black oak had significantly higher removal probabilities than other species in six and five comparisons, respectively (Figure A.1). Nuttall and willow oak had significantly lower removal probabilities in six and three comparisons, respectively. Suggesting that of the choices available, southern red and black oak, which are upland oak species, were most preferred by seed predators, and Nuttall and willow oak, which are bottomland oak species, were most avoided. All other acorn species were not different, but the direction of these comparisons was mixed within species for cherrybark, northern red, scarlet, and Shumard. However, there appeared no trend in removal probability across the two groupings of oaks by site characteristics (i.e. upland vs. bottomland) when considering results from all species because many species had mixed effects on removal probability when compared to species from the other group.

Pairwise comparisons for the caching seed predator interaction with treatment produced fewer significant comparisons but more consistent effects of selection within species (Table A.1). Black, cherrybark, and southern red oak had higher removal probabilities in all significant comparisons, suggesting they were selected for by caching seed predators. Northern red, Nuttall, scarlet, and Shumard had lower removal probabilities in all significant comparisons, suggesting they were selected against by caching seed predators.
Discussion

My findings suggest that acorn exposure to fire generates differential indirect effects on selection by caching and non-caching seed predators that affect the rate at which acorns are removed. Fire significantly delayed time to removal for burned acorns similar to observations by Greenler et al. (2019). They reported reduced acorn removal rates by small mammals in burned stands compared to controls in central Indiana; however, fires were implemented two years prior to their observations, and they hypothesized the effect on acorn removal was driven by changes in plant community structure. My study controlled for confounding changes in the environment by only exposing acorns to fire, homogenizing offerings of acorns to predators, and randomizing sites. This design allowed me to isolate another mechanism, that fire indirectly affects acorn removal by affecting seed predator preferences. The change in acorn removal probability could have important implications for acorn success rates, because while many acorns are typically consumed by seed predators there are typically still a percentage surviving until spring (Haas and Heske 2005, Sork 1993). A change in the rate at which acorns are removed could increase the percentage persisting to spring and thus increase the probability of acorns successfully germinating and producing seedlings.

Non-caching seed predators reduced the effect of fire on acorn removal rates, suggesting that they did not preferentially remove acorns from either treatment. Since non-caching seed predators in my study were unselective of treatment, increased use of stands following fire via the magnet effect could negatively affect overall acorn success. For example, Westlake et al. (2020) observed a significant increase in use of burned patches by deer 45 days following fire, which would increase opportunity for acorn removal by this large non-caching seed predator and could greatly decrease the number of acorns persisting through winter. My data show little
evidence for selection of treatment by caching seed predators, but acorn removal by caching seed predators is often reduced by effects of fire on understory vegetation, affecting selection of microhabitats by small mammals (Greenler et al. 2019, Kennedy and Peter 2005, Pérez-Ramos and Marañón 2008). This too could affect acorn success in burned stands as a reduction in removals by caching seed predators may increase the number consumed by non-caching predators with no chance of surviving removal.

The highly controlled design of my study allowed me to isolate the indirect effect of fire on removal of acorns by seed predators, but fire may affect acorn success by changing the environment. The relatively controlled but unnatural setting of acorns in sand covered plastic trays could have affected the perception of acorns by seed predators in my study, but this design was essential to homogenizing visibility of acorns across plots. Moreover, the design was identical between treatments and we observed wildlife approaching and removing acorns from arrays relatively quickly after establishment. Thus, we do not believe this potential flaw in design confounded our interpretations of results for this experiment. However, it is important to realize that these factors limit more broad sweeping inferences of net fire effects on oak success via this mechanism. For example, we controlled for changes in the landscape that affect acorn vulnerability following prescribed fire, but the reduction in fuel loads and charring of the soil and acorn surface could affect acorn detection by seed predators and thus may change the outcome of our experiment. However, this study was intended to be a proof of concept that fire could indirectly affect the fate of acorns by influencing interactions with consumers and my controlled design allowed me to isolate that factor and demonstrate that likelihood. Thus, my experiment indicates that indirect effects of fires on species interactions should be considered in future research evaluating the net effects of fire on oak regeneration success.
Use of camera traps recording video allowed me to observe seed predators visiting plots and removing acorns, but some acorns were removed by unobserved predators because of imperfect detection. Unobserved removals were not equal between treatments and were two-fold higher in unburned acorn treatment plots at both study sites. This did not influence the overarching conclusion that fire decreased hazard, because all cameras were programmed to trigger automatically to provide recurring assessments of acorn persistence, regardless of wildlife detection. However, because caching seed predators tended to be smaller and thus, less detectable, inferences concerning the relative role of cachers in removal could have been influenced. I explored this issue by discarding four sites with high incidence of unobserved acorn removals and reanalyzing the data, but this had little effect on the direction of inference. Thus, I am confident that my interpretation of results were robust to this issue.

My results suggest there is an indirect effect of fire exposure to acorns that reduces the rate at which acorns are removed by seed predators. On a forest stand scale, vegetation structure and the magnet effect may affect seed predator use of patches and further complicate the relationship of fire and removal by predators (Allred et al. 2011, Archibald et al. 2005, Greenler et al. 2019, Kennedy and Peter 2005, Klop et al. 2007, Pearson et al. 1995, Pérez-Ramos and Marañón 2008, Westlake et al. 2020). Acorn production varies across years and among trees (Brooke et al. 2019, Lashley et al. 2009), which could affect removal rates if there were a density dependent response by seed predators. Small mammal populations are usually unaffected or slightly increased following low to moderate intensity prescribed fire, which should have a minimal effect on removal (Ford et al. 1999, Nelson et al. 2017, Raybuck et al. 2012). Prescribed fire often varies in intensity, creating mosaics of unburned and burned patches, which will affect intensity of fire effects on acorns (Lertzman et al. 1998). These confounding effects may change
the magnitude or direction of effects I observed, further adding complexity to the effects of fall fire on acorn success. Thus, future experiments could build off my work and the work of others by incorporating environmental changes and species interactions into field observations and analyses.

**Conclusions**

My results have important implications for oak regeneration in forests where prescribed fire is being implemented in the dormant season. Burned acorns experienced a lower probability of removal than unburned acorns in my study. This decrease in the probability of removal over time could increase the number of acorns persisting until spring germination, particularly in systems where predators are already satiated, and this effect would accentuate satiation. The decrease in treatment effect by both predator functional groups suggests that fire does not greatly affect selection by functional groups. However, in a managed forest, the magnet effect and microhabitat selection of small mammals following fire could cause a shift in removal of acorns to non-caching seed predators following fire, reducing the probability of acorns persisting until spring by reducing opportunities to be cached. To fully evaluate the effects of fire on acorn success in managed forests, future research should measure effects of fire on predator removal and caching rates in burned forest patches.
Figure 2.1 Coefficients for highest ranked Cox mixed regression model

Coefficient estimates with 95% confidence intervals for significant variables in the top ranked Cox mixed regression model. Treatment significantly increased the probability of acorn removal in control plots (Coeff. = 2.817, p < 0.01). Caching predator presence had a significant interaction with treatment that decreased the treatment effect (Coeff. = -0.845, p < 0.01). Non-caching predator presence had a significant interaction with treatment that decreased the treatment effect (Coeff. = -1.906, p < 0.01).
Figure 2.2  Persistence probability of acorns in treatment plots

Estimated persistence probability over time for acorns tested in predator removal plots across both study sites. Burned acorns had a greater persistence probability than unburned acorns over my study period. Persistence probability is on the y-axis, days on the x-axis, colors specify treatment (blue = burned, yellow = unburned), and shaded area represents 95% confidence intervals.
Literature Cited


28


CHAPTER III
FACULTATIVE SEED PREDATORS DRIVE COMMUNITY-LEVEL INDIRECT EFFECTS OF MAST SEEDING

Introduction

A resource pulse is a low-frequency, short-term increase in resource availability concentrated in space and time (Ostfeld and Keesing 2000, Yang et al. 2008). Although relatively rare, resource pulses can have unique consequences for life cycles and behavior of individual consumers, stimulate numerical responses at the population level, and generate indirect effects at the community level (Yang et al. 2008). Indirect effects to communities commonly include direct and indirect bottom-up effects followed by delayed top-down effects (Ostfeld and Keesing 2000). These can arise from a variety of mechanisms, but in general indirect effects often result from numerical or behavioral responses of facultative consumers or their facultative predators because these organisms interact with a large portion of the community and are able to diet switch when the resource is depleted (see Yang et al. 2008). For example, carrion attracts facultative avian and mammalian scavengers which increase predation on alternative prey near carrion sites (Wilmers et al. 2003), and extreme levels of carrion can generate indirect effects from sequential behavioral responses of facultative predators to increased abundance of obligate scavengers (Lashley et al. 2018).

Mast seeding is a resource pulse resulting from a reproductive strategy employed by many perennial plants in which the seed production cycle is synchronized within populations and
highly variable from year to year (Crone and Rapp 2014, Kelly 1994). Years of high yield in mast seeding plants generate effects similar to other types of resource pulses (Ostfeld and Keesing 2000, Yang et al. 2008). For example, mast seeding in oaks (Quercus spp.) and beeches (Nothofagus spp.) causes a numerical response in small mammals that attract avian and mammalian predators, strengthening apparent competition between those small mammals and alternative prey of their predators (e.g., Elliott et al. 1996; King 1983; Murphy and Dowding 1995; O'Donnell and Phillipson 1996; O'Donnell 1996; Schmidt 2003; Schmidt and Ostfeld 2003, 2008). In each of those examples, the observed indirect effects were a result of diet switching by a facultative consumer. Oaks have a particularly high potential to generate these types of indirect effects that structure communities because their seeds (i.e., acorns) are an important food for a wide array of taxa (Martin et al. 1961, McShea et al. 2007).

Most studies have focused on the evolutionary significance of mast seeding rather than characterizing community-level effects. The predator satiation hypothesis (PSH) is the most popular and widely tested hypothesis providing an evolutionary explanation of mast seeding (e.g., Bogdziewicz et al. 2018a, 2018b; Greenberg and Zarnoch 2018; Kelly 1994). The PSH posits that synchronous conspecific seeding cycles starve specialized seed predators during poor mast years and then overwhelm those predators with mast events, leading to positive density-dependent seed survival (Janzen 1971, Silvertown 1980). Research on oak masting ecology has primarily explored how mechanisms associated with mast seeding affect oak fitness through this positive density-dependent mechanism (Bogdziewicz et al. 2018a, 2018b; Crawley and Long 1995, Greenberg and Zarnoch 2018; Sork 1993). At some threshold, which may be caused by handling time or satiety, the increase in acorn density causes deaccelerating intake by seed predators, and the linear relationship plateaus in a type II or III functional response (Fletcher et
al. 2010). However, the same functional response from facultative seed predators, which are also herbivores, can cause negative density-dependent effects on seedlings near the parent tree (Connell 1971, Janzen 1970, Zhang et al. 2020).

Although annual population growth rates for some acorn predators, such as seed caching rodents and carpophagous insects, may depend upon the amount of mast produced in a given year, populations of generalist facultative seed predators, such as white-tailed deer (*Odocoileus virginianus*; hereafter deer) are relatively independent of masting cycles. Deer are one of the most important vertebrate predators of acorns in North America (Steiner 1996), with fall diets primarily composed of acorns during good mast years (Harlow et al. 1975, McShea and Schwede 1993, McCullough 1985, Steiner 1996). Also, deer readily diet switch or change behavior when acorns are scarce, allowing them to maintain stable populations through poor mast years (Harlow et al. 1975, McCullough 1985). For example, McShea and Schwede (1993) reported deer expanded and shifted their home ranges to oak-hickory forests in fall during years when mast production was high but favored other food types in poor acorn production years. Deer likely have a strong effect on oak fitness by consuming acorns, especially given that they can remain abundant during poor mast years (Harlow et al. 1975, Steiner 1996). Likewise, deer may also affect oak fitness in the seedling life stage and affect overall plant community composition given that they readily eat dozens of other plant species common in oak forests (Lashley et al. 2011).

I designed an acorn addition experiment to test a series of hypotheses regarding whether oak masting affects consumer activity near parent trees, satiates seed predators, and indirectly impacts local plant communities via shifts in consumer behavior. First, I used camera traps to monitor deer activity to test the hypothesis that acorn additions would cause a shift in consumer behavior. Second, I marked acorns and tracked their fate to test the hypothesis that masting
generates positive density-dependent seed survival. Third, I transplanted oak and blackgum
(Nyssa sylvatica), a common competing species in eastern forests (Iverson et al. 2008, Nowacki
and Abrams 2008, Sutherland and Hutchinson 2003), seedlings into each plot to test the
hypothesis that masting would generate either negative density-dependent growth on oak
seedlings or strengthen deer-mediated apparent competition with blackgum (i.e., oak mast
seeding attracts shared enemy that suppresses relative growth of competing blackgum seedlings).
Finally, I characterized the local plant community in plots with and without acorn additions to
test the hypothesis that mast seeding would elevate local herbivory pressure, thus providing a
spatiotemporal niche opportunity for herbivory tolerant plants and causing the communities to
diverge in structure.

Materials and Methods

Study Site

The experiment was conducted on Spirit Hill Farm, a 492 ha property in Tate and
Marshall Counties in northwestern Mississippi, USA. This region is characterized by the upper
thick loess hills, primarily wind-blown material deposited east of the Mississippi Alluvial Valley
consisting of silt and silt loam. Average annual precipitation is 145.9 cm, average temperature is
15.1 °C, and average low and high temperatures are 7.9 °C and 22.3 °C respectively (U.S.
Climate Data, 2020). The property includes approximately 140 ha of temperate mixed upland
hardwood forest with a substantial oak component, including white oak (Q. alba), Shumard oak
(Q. shumardii), black oak (Q. velutina), scarlet oak (Q. coccinia), southern red oak (Q. falcata),
post oak (Q. stellata) and cherrybark oak (Q. pagoda). A non-oak hardwood component is also
present in the midstory, including sweetgum (Liquidambar styraciflua), blackgum, red maple
(Acer rubrum), and winged elm (Ulmus alata). Forest stands are separated by mixed bahiagrass (Paspalum notatum) pastures and row crop agriculture.

**Experimental Design**

In September 2018, 50 southern red oak trees with diameters at breast height (DBH) ranging 29-90 cm were selected as “parent trees” across four upland hardwood stands. Trees were paired with others similar in DBH and growing within 50 m of each other, making 25 parent tree pairs. Crown diameters of 10 random southern red oaks in the same forest stands were measured at a random azimuth and again at a 90° angle to the original measurement to estimate mean canopy diameters.

Circular plots, equal in diameter to the estimated stand mean tree canopy size (11 m), were established under the 50 parent trees with the outer edge of each plot bordering one side of the main stem (Figure 3.1). In October 2018, a rapid mast survey was conducted to estimate the relative abundance of acorns in tree canopies over plots (Koenig et al. 1994). Because selected parent trees were in upland hardwood stands with a prominent oak component, total acorn producing canopy over plots was surveyed, including non-parent oak trees overlapping plots. In each pair, the plot with less relative acorn abundance was selected as the control plot.

In each plot, I transplanted two blackgum (basal diameter = 67.9 ± 1.3, stem length = 763.5 ± 25.6) and two Shumard oak (basal diameter = 56.7 ± 1.1, stem length = 433.5 ± 13.1) greenhouse reared seedlings. Seedlings were planted in random order and configurations 1 m apart and tagged with wire loop tags with unique identification numbers. I set a camera trap (Bushnell Trophy Cam HD) on a 1-minute photo delay and “normal” PIR sensor mode oriented parallel to the ground and 0.5 m up the main stem of each parent tree to monitor deer use of plots. Pin flags were placed 5 m in front of cameras to establish a set camera trap detection area.
to standardize area monitored by cameras in each plot. All saplings were removed between cameras and 5 m pin flags to standardize detection opportunity for each camera.

Seventy-five thousand Shumard oak acorns were collected across Mississippi State University’s campus and Starkville, MS, USA from mid-October to mid-November and stored in burlap bags in refrigerated storage at 4 °C until use. Average number of acorns per gallon (500) was measured by counting acorns per gallon from 10 different cohorts of acorns collected; this estimate was also later used to measure the number of acorns added to plots. Percent viable acorns (72%) was estimated by sampling 10 random samples of 10 acorns from 10 different collected cohorts of acorns (n = 1,000) using the acorn viability inspection method described by Morina et al. (2017).

Over three weeks in early November 2018, 3,000 acorns were distributed under each of the selected acorn addition parent trees to achieve a density of 31.5 acorns per m² of canopy, typical of average mast crops by red oak species (Auchmoody et al. 1993, Beck and Olson 1968). Acorns were haphazardly distributed by hand every seven days while standing at plot center. Five-hundred acorns were added the first week, two-thousand the second week, and five-hundred the third, to simulate a normal distribution of seed addition (Burns et al. 1954). Control plots were also visited on acorn addition days, to avoid any biases among plots generated by human visitation. On the first day of acorn addition, I distributed 30 marked acorns in a 2-m² area in the center of all plots. I marked the acorns by painting a black dot on their accession point using a permanent marker prior to distribution which is a standard technique for monitoring acorn depredation (Brooke et al. 2019).
Data Collection

Two-minute standardized searches were conducted in each plot in late March to recover marked acorns from plots. Total stem lengths of planted seedlings were measured in March and again in September. Differences in stem length from the beginning to end of the growing season (i.e., March to September) for all seedlings were then divided by their initial March stem length and averaged between the two seedlings by species for each plot. The blackgum average was subtracted from oak in each plot to calculate the effect of acorn addition on relative growth of oak and blackgum. For camera trap images I recorded time, date, animal location, species, sex, age, posture, and feeding status. Intensity of deer use was estimated for each plot by summing the number of deer observed feeding in images within 5 m of the camera during the experimental period (Nov. 3, 2018 – Mar. 29, 2019).

Additionally, during August 2019 I conducted point-intercept vegetation surveys in all plots. Surveys consisted of two 10 m vegetation transects situated at random Azimuths perpendicular to one another in each plot. Using a 1.5 m Robel pole, all species intersecting the pole at each point 0.5m along transects was recorded. Plant community data was classified by the following growth forms: forbs, trees/shrubs, vines, and graminoids (rushes, sedges, grasses) and total number of detections of each growth form were calculated for each plot.

Data Analysis

All analyses were conducted in R version 3.5.1 and R studio version 1.2.5001. I used function glm.nb in the MASS package to conduct generalized linear models with a negative binomial distribution to examine the relationship between acorn addition and four response variables: total deer feeding detections, raccoon (Procyon lotor) detections, eastern grey squirrel (Sciurus carolinensis) detections, and all seed predator detections other than deer. I chose
negative binomial distributions because of overdispersion in the data which had no upper limit. Using data from acorns recovered during timed searches, I then used the glmer function to create a binomial generalized linear model with tree pair as a random effect to compare apparent acorn survival between treatments. While acorn detection during timed searches was likely not 100%, detection probability should be constant between treatments, yielding an accurate index of acorn survival for both treatments.

I used a linear mixed model (lmer) with tree pair as a random effect to test treatment effects on relative stem length growth for oak, blackgum, and oak-blackgum; excluding 11 seedlings (eight blackgum and three oak), which had been girdled by rabbits close to the ground and experienced considerably more stem growth than those not girdled by rabbits. I then conducted generalized linear models (glm) using Poisson distributions to test for treatment effects on coverage by different growth forms in each plot. Next, I used the manyglm function in package mvabund to run generalized linear models with a Poisson distribution and plot as a random effect to test for differences in plant communities between treatments using species identity. After developing the models, I assessed significance using the anova function from the stats package to generate an analysis of deviance table with adjusted p values (Wang et al., 2012). Finally, I used function specaccum in package vegan to create species accumulation curves with the rarefaction method (Oksanen et al. 2010). Then, I plotted these curves with standard deviation using package ggplot2.

**Results**

In support of my hypothesis that acorn additions would cause a change in behavior of consumers, deer use was 441% greater in acorn addition than control plots ($z = 7.202$, $p < 0.001$, Figure 3.2 A and B). I was unable to detect a significant relationship between treatment and
detections of raccoon \( (z = 1.079, p = 0.281) \), eastern grey squirrel \( (z = 1.120, p = 0.263) \), and all non-deer seed predators combined \( (z = 0.712, p = 0.477) \): bluejay \( (Cyanocitta cristata) \), eastern grey squirrel, mice \( (Peromyscus \text{ spp.}) \), southern flying squirrel \( (Glaucomys volans) \), fox squirrel \( (Sciurus niger) \), Virginia opossum \( (Didelphis virginiana) \), raccoon, wild turkey \( (Meleagris gallopavo) \). In support of my hypothesis that acorn additions would cause positive density-dependent survival of seeds, apparent survival of marked acorns was greater in acorn addition \( (0.26\% \text{ were recovered}) \) than in control plots \( (3\% \text{ were recovered}) \) \( (z = 3.388, p < 0.001) \). Relative growth of oak seedlings tended to be lower in acorn addition plots \( (t = 1.323, p = 0.203) \), and relative growth of blackgum seedlings tended to be higher in acorn addition plots \( (t = -1.026, p = 0.311) \). However, when considering treatment effects on both seedlings together, the difference in relative stem growth between oak and blackgum seedlings was significant and showed a negative effect of acorn additions on the relationship of oak to blackgum \( (t = 2.038, p = 0.057, \text{Figure 3.3}) \).

I detected 63 plant species in plant community surveys: 20 trees/shrubs, 9 vines, 26 forbs, and 8 graminoids. Control plots contained 52 species, of which 21 were unique to treatment; acorn addition plots contained 42 species, including 11 unique to treatment. In support of my hypothesis \( (\text{Figure 3.2 } C) \), community composition differed in acorn addition plots from control plots \( (\text{LRT} = 122.6, p = 0.036) \). This pattern appeared to be driven by changes in the coverage of forbs \( (z = 2.373, p = 0.017) \) and graminoids \( (z = 3.747, p < 0.001) \), with control plots having 59\% more forb cover and 31\% more cover of graminoids than acorn addition plots. I failed to detect any significant difference in cover of vines \( (z = 0.173, p = 0.863) \) or trees/shrubs \( (z = 1.241, p = 0.215) \). As a result of these local changes in plant community, the overall
accumulation of species (i.e., beta diversity) was greater when considering acorn addition and control plots than with either plot alone (Figure 3.2 D).

**Discussion**

My data provide support for an important link between resource pulses and the broader community diversity generated through the functional response of facultative consumers that promotes coexistence in understory vegetation assemblages. Consumer interactions are important to food webs and have been implicated as mediators promoting coexistence mechanisms in other systems. For example, snails (*Helix aspersa*) affect competitive relationships between *Trifolium* species, promoting coexistence of *T. pratense* and *T. repense* through herbivory (Hanley and Sykes 2009), and pteromalid wasps (*Anisopteromalus calandrae*) promote coexistence of bruchid beetles via frequency-dependent predation (Ishii and Shimada 2012). While the underlying mechanisms vary somewhat between systems, consumers interact with a relatively large portion of the community by mediating effects of resource pulses on other trophic levels (Yang et al. 2008), and are thus the fabric linking important phenomena to the structure and function of the broader community. Similarly, my results suggest facultative consumers of acorns may be the conduit linking resource pulses from oaks to diversity of the broader hardwood forest plant communities.

The bottom-up effect of mast as a resource pulse creates a spatiotemporal response by facultative seed predators, driving indirect effects on the community. Acorn additions in my experiment generated a behavioral response in deer use comparable to that found by McShea and Schwede (1993), who observed increased intensity of deer use in oak-hickory forest during mast years. My data indicate that deer were the primary consumer generating indirect effects of mast seeding, given I did not observe a functional response in other species. In my study system there
are two primary mechanisms by which deer may have affected plant community assemblages. The first mechanism is biopedturbation, a soil disturbance caused by organisms that promotes heterogeneity in plant communities via patchiness of soil conditions (Whitford and Kay 1999), which could have arisen from increased deer traffic in plots and likely would have the greatest effect on annual plants through effects on the seedbed. The second mechanism is a top-down effect produced via selective herbivory by deer affecting plant community composition, which has been demonstrated in numerous systems (Russell et al. 2001) and would primarily affect perennial plants persisting through winter. My data suggest that acorn additions strengthened the top-down effect of deer on plant communities via herbivory, because plant community changes were driven primarily by perennial plants, that would likely be less effected by biopedturbation than herbivory. The reduction in species richness I observed in acorn addition plots was consistent with Abrams and Johnson (2012), who found a significant increase in species richness when deer were excluded from plots in southeastern Pennsylvania. Interestingly, while deer effects on tree seedlings, shrubs, and vines have primarily been identified as the driving effects on species richness (Abrams and Johnson 2012, Gill and Beardall 2001), changes in plant cover between treatments were only significant for graminoids and forbs in my study.

The functional response of facultative seed predators also has important direct implications for oak propagule success through acorn depredation and herbivory on seedlings. Despite the significant behavioral response by deer, I observed a positive density-dependent relationship between acorn density and acorn survival. Positive density-dependence of seeds, an important element of PSH (Boucher 1985), is well supported in mast seeding plants across temperate and tropical forests in several families of perennial plants (Boucher 1981, Crawley and Long 1995, Kelly and Sullivan 1997, Zwolak et al. 2016). Numerous other empirical studies
indicate predator satiation as a valuable strategy for acorn survival to varying degrees depending on conspecific tree density, hatching rates of acorn specialist insects, oak density, and consistency of acorn production (Bogdziewicz et al. 2018b, Crawley and Long 1995). I also observed decreased growth of oak seedlings relative to heterospecific seedlings (i.e., blackgum), which was associated with activity of deer, as facultative seed predators, who likely increased herbivory pressure near parent trees when responding to acorn availability. Negative density dependence of plant propagules was proposed by Janzen (1970) and Connell (1971) in tropical forests as a mechanism to maintain tree species diversity. My results agree with other studies indicating that evidence for the Janzen-Connell Hypothesis is stronger for seedlings than for seeds (Comita et al. 2014, Connell 1971, Hyatt 2003, Johnson et al. 2012). These two conflicting effects on the competitive relationship between oaks and heterospecific seedlings provide evidence for the PSH and Janzen-Connell Hypothesis in the presence of a large magnitude response by a facultative seed predator.

Observed direct and indirect effects in my study have important implications for the conservation of oaks. Oaks are declining in dominance across eastern North America because (1) a bottleneck in the regeneration cycle creates a buildup of seedlings in the understory that are not advancing into the midstory (Abrams 1992, Aldrich et al. 2005, Fei et al. 2011, McShea et al. 2007, McWilliams et al. 2002, Moser et al. 2006, Spetich et al. 2011), and (2) fire exclusion creates a feedback loop that promotes non-oak hardwoods and further shifts forests toward alternative stable states that suppress fire (i.e. mesophication, Nowacki and Abrams 2008). The positive density-dependence I observed in acorn survival in masting year conditions is important for the provision of viable acorns to spring germination. My seedling data, however, suggests that conspecific heterogeneity in seed production among masting oaks (Brooke et al. 2019,
Lashley et al. 2009) is important for oak regeneration success because trees with little mast production create refugia from spatiotemporal variation in deer herbivory due to oak masting. On the other hand, trees that produce large acorn crops experience increased deer use that produces an environment more conducive to the growth of non-oak hardwood seedlings like blackgum and suppresses oak seedlings, which could further exacerbate mesophication by promoting seedling growth of mesophytic species.

Management Implications

My results have important implications for resource managers wishing to promote oak forest regeneration, wildlife, and plant community diversity. Previous studies indicate a third of oak trees produce approximately 75% of all acorns, underlining the value of certain trees within oak stands as mast producers (Brooke et al. 2019, Lashley et al. 2009). As my data show, the ability of these masting oaks to promote acorn survival through predator satiation accentuates their value in forests where managers wish to promote oak regeneration. Brooke et al. (2019) demonstrated how managers can promote acorn production by observing trees during mast years to identify the better mast producers and then releasing these trees from competition via forest stand improvement to increase the number of acorns each tree produces. Increased acorn production improves not only the amount of mast available in fall and winter for various wildlife species, but also seed survival via predator satiation. However, there appears to be a reduction in competitive advantage of oak seedlings relative to some non-oak competing species under masting trees. Retaining poor seed producing oaks in forests may provide value through heterogeneity in deer use which promotes species richness in plant communities and refugia for conspecific seedlings. As managers work to release better masting oaks, effort should also be given to retain some non-oak trees with wildlife value that promote species richness both through
their retention in the overstory but also through cascading effects of herbivores on plant communities.
Experimental plots were 11 m in diameter, based off average southern red oak crown diameter in the forest. Plots were placed directly below parent trees with mainstem of the parent southern red oak (*Quercus falcata*) on plot edge. Two blackgum (*Nyssa sylvatica*) and two Shumard oak (*Quercus shumardii*) seedlings were planted within the dripline portion of plot. A camera trap was placed on the parent tree overlooking plot and a pin flag was placed 5 m in front of the camera; deer detections were recorded within 5 m to standardize area observed by cameras.
Figure 3.2  Conceptual deer use, deer feeding detections, conceptual plant cover, and species accumulation by treatment and among acorn addition treatments

A) Conceptual depiction of deer use as a function of masting. B) Average deer feeding detections by week of year for both treatments. C) Conceptual map of plant cover based off masting and deer activity. D) Species accumulation curves for each treatment and both combined per meter of transect.
Relative growth of seedlings represents a negative effect of acorn additions on the competitive relationship of Shumard oak (*Quercus shumardii*) to blackgum (*Nyssa sylvatica*). Relative growth was calculated by first dividing stem length change over summer by initial stem length for all seedlings and calculating an average among seedlings of each species in all plots, the relative stem length growth of oak was then subtracted by relative stem length growth of blackgum.
Literature Cited


APPENDIX A

SUPPLEMENTAL RESULTS OF PAIRWISE COMPARISONS FOR SIGNIFICANT
INTERACTION TERMS WITHIN COX MIXED REGRESSION MODELS
Figure A.1  Pairwise comparisons between acorn species from highest ranked model

Pairwise comparisons of acorn species from study sites. Black oak and southern red oak had significantly higher removal probabilities than other species in all significant comparisons. Nuttall and willow had significantly lower removal probabilities than other species in all significant comparisons.
Table A.1  Pairwise comparisons of acorn species removal probabilities from highest ranked model without (= 0) and with (= 1) caching predator presence.

<table>
<thead>
<tr>
<th></th>
<th>( \beta )</th>
<th>SE</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>cherrybark.0 - black.0</td>
<td>-0.345361</td>
<td>0.151522</td>
<td>-2.279</td>
<td>0.6328</td>
</tr>
<tr>
<td>northern_red.0 - black.0</td>
<td>-0.629145</td>
<td>0.157406</td>
<td>-3.997</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>nuttall.0 - black.0</td>
<td>-1.36384</td>
<td>0.160944</td>
<td>-8.474</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>scarlet.0 - black.0</td>
<td>-0.639842</td>
<td>0.156325</td>
<td>-4.093</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>shumard.0 - black.0</td>
<td>-0.989037</td>
<td>0.155716</td>
<td>-6.352</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>southern_red.0 - black.0</td>
<td>0.161135</td>
<td>0.143997</td>
<td>1.119</td>
<td>0.9992</td>
</tr>
<tr>
<td>willow.0 - black.0</td>
<td>-0.780046</td>
<td>0.153921</td>
<td>-5.068</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>black.0 - black.0</td>
<td>1.046501</td>
<td>0.154824</td>
<td>6.759</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>cherrybark.1 - black.0</td>
<td>0.935505</td>
<td>0.151745</td>
<td>6.165</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>northern_red.1 - black.0</td>
<td>0.427217</td>
<td>0.153585</td>
<td>2.782</td>
<td>0.2736</td>
</tr>
<tr>
<td>nuttall.1 - black.0</td>
<td>0.305465</td>
<td>0.153084</td>
<td>1.995</td>
<td>0.823</td>
</tr>
<tr>
<td>scarlet.1 - black.0</td>
<td>0.436212</td>
<td>0.154511</td>
<td>2.823</td>
<td>0.2507</td>
</tr>
<tr>
<td>shumard.1 - black.0</td>
<td>0.699948</td>
<td>0.152263</td>
<td>4.597</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>southern_red.1 - black.0</td>
<td>1.180935</td>
<td>0.157804</td>
<td>7.484</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.1 - black.0</td>
<td>0.41635</td>
<td>0.16266</td>
<td>2.56</td>
<td>0.4213</td>
</tr>
<tr>
<td>northern_red.0 - cherrybark.0</td>
<td>-0.283784</td>
<td>0.163822</td>
<td>-1.732</td>
<td>0.9357</td>
</tr>
<tr>
<td>nuttall.0 - cherrybark.0</td>
<td>-1.018478</td>
<td>0.164862</td>
<td>-6.178</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>scarlet.0 - cherrybark.0</td>
<td>-0.294481</td>
<td>0.162429</td>
<td>-1.813</td>
<td>0.09</td>
</tr>
<tr>
<td>shumard.0 - cherrybark.0</td>
<td>-0.643675</td>
<td>0.16026</td>
<td>-4.016</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>southern_red.0 - cherrybark.0</td>
<td>0.506496</td>
<td>0.150839</td>
<td>3.358</td>
<td>0.0601</td>
</tr>
<tr>
<td>willow.0 - cherrybark.0</td>
<td>-0.434685</td>
<td>0.158345</td>
<td>-2.745</td>
<td>0.2964</td>
</tr>
<tr>
<td>black.1 - cherrybark.0</td>
<td>1.391863</td>
<td>0.161792</td>
<td>8.603</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>cherrybark.1 - cherrybark.0</td>
<td>1.280866</td>
<td>0.157678</td>
<td>8.123</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>northern_red.1 - cherrybark.0</td>
<td>0.772578</td>
<td>0.160739</td>
<td>4.806</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>nuttall.1 - cherrybark.0</td>
<td>0.650827</td>
<td>0.159693</td>
<td>4.075</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>scarlet.1 - cherrybark.0</td>
<td>0.781573</td>
<td>0.161388</td>
<td>4.843</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>shumard.1 - cherrybark.0</td>
<td>1.045309</td>
<td>0.159281</td>
<td>6.563</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>southern_red.1 - cherrybark.0</td>
<td>1.526296</td>
<td>0.164492</td>
<td>9.279</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.1 - cherrybark.0</td>
<td>0.761712</td>
<td>0.168285</td>
<td>4.526</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>nuttall.0 - northern_red.0</td>
<td>-0.734695</td>
<td>0.168668</td>
<td>-4.356</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>scarlet.0 - northern_red.0</td>
<td>-0.010697</td>
<td>0.165809</td>
<td>-0.065</td>
<td>1</td>
</tr>
<tr>
<td>shumard.0 - northern_red.0</td>
<td>-0.359892</td>
<td>0.162431</td>
<td>-2.216</td>
<td>0.6793</td>
</tr>
<tr>
<td>southern_red.0 - northern_red.0</td>
<td>0.79028</td>
<td>0.156232</td>
<td>5.058</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.0 - northern_red.0</td>
<td>-0.150901</td>
<td>0.163238</td>
<td>-0.924</td>
<td>0.9999</td>
</tr>
<tr>
<td>black.1 - northern_red.0</td>
<td>1.675646</td>
<td>0.165997</td>
<td>10.094</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>cherrybark.1 - northern_red.0</td>
<td>1.56465</td>
<td>0.163481</td>
<td>9.571</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>northern_red.1 - northern_red.0</td>
<td>1.056362</td>
<td>0.163449</td>
<td>6.463</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>nuttall.1 - northern_red.0</td>
<td>0.93461</td>
<td>0.163568</td>
<td>5.714</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>scarlet.1 - northern_red.0</td>
<td>1.065357</td>
<td>0.164662</td>
<td>6.47</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>shumard.1 - northern_red.0</td>
<td>1.329093</td>
<td>0.162983</td>
<td>8.155</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>southern_red.1 - northern_red.0</td>
<td>1.81008</td>
<td>0.169056</td>
<td>10.707</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.1 - northern_red.0</td>
<td>1.045496</td>
<td>0.17258</td>
<td>6.058</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>β</td>
<td>SE</td>
<td>Z</td>
<td>P</td>
</tr>
<tr>
<td>--------------------</td>
<td>---------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
</tr>
<tr>
<td>scarlet.0 - nuttall.0 == 0</td>
<td>0.723998</td>
<td>0.165917</td>
<td>4.364</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>shumard.0 - nuttall.0 == 0</td>
<td>0.374803</td>
<td>0.158797</td>
<td>2.36</td>
<td>0.5709</td>
</tr>
<tr>
<td>southern_red.0 - nuttall.0 == 0</td>
<td>1.524974</td>
<td>0.159421</td>
<td>9.566</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.0 - nuttall.0 == 0</td>
<td>0.583793</td>
<td>0.158583</td>
<td>3.681</td>
<td>0.0208</td>
</tr>
<tr>
<td>black.1 - nuttall.0 == 0</td>
<td>2.410341</td>
<td>0.167424</td>
<td>14.397</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>cherrybark.1 - nuttall.0 == 0</td>
<td>2.299345</td>
<td>0.163836</td>
<td>14.034</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>northern_red.1 - nuttall.0 == 0</td>
<td>1.791057</td>
<td>0.164956</td>
<td>10.858</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>nuttall.1 - nuttall.0 == 0</td>
<td>1.669305</td>
<td>0.163855</td>
<td>10.188</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>shumard.1 - nuttall.0 == 0</td>
<td>2.063788</td>
<td>0.164232</td>
<td>12.566</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>southern_red.1 - nuttall.0 == 0</td>
<td>2.544774</td>
<td>0.170363</td>
<td>14.937</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.1 - nuttall.0 == 0</td>
<td>1.78019</td>
<td>0.172098</td>
<td>10.344</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>shumard.0 - scarlet.0 == 0</td>
<td>-0.349195</td>
<td>0.16198</td>
<td>-2.156</td>
<td>0.7215</td>
</tr>
<tr>
<td>southern_red.0 - scarlet.0 == 0</td>
<td>0.800976</td>
<td>0.154688</td>
<td>5.178</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.0 - scarlet.0 == 0</td>
<td>-0.140204</td>
<td>0.160295</td>
<td>-0.875</td>
<td>1</td>
</tr>
<tr>
<td>black.1 - scarlet.0 == 0</td>
<td>1.686343</td>
<td>0.162781</td>
<td>10.36</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>cherrybark.1 - scarlet.0 == 0</td>
<td>1.575347</td>
<td>0.159854</td>
<td>9.855</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>northern_red.1 - scarlet.0 == 0</td>
<td>1.067059</td>
<td>0.160575</td>
<td>6.645</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>nuttall.1 - scarlet.0 == 0</td>
<td>0.945307</td>
<td>0.160272</td>
<td>5.898</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>scarlet.1 - scarlet.0 == 0</td>
<td>1.076053</td>
<td>0.160871</td>
<td>6.689</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>shumard.1 - scarlet.0 == 0</td>
<td>1.33979</td>
<td>0.159794</td>
<td>8.385</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>southern_red.1 - scarlet.0 == 0</td>
<td>1.820777</td>
<td>0.165621</td>
<td>10.994</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.1 - scarlet.0 == 0</td>
<td>1.056192</td>
<td>0.168731</td>
<td>6.26</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>southern_red.0 - shumard.0 == 0</td>
<td>1.150171</td>
<td>0.152937</td>
<td>7.521</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.0 - shumard.0 == 0</td>
<td>0.20899</td>
<td>0.155314</td>
<td>1.346</td>
<td>0.9939</td>
</tr>
<tr>
<td>black.1 - shumard.0 == 0</td>
<td>2.035538</td>
<td>0.164784</td>
<td>12.353</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>cherrybark.1 - shumard.0 == 0</td>
<td>1.924542</td>
<td>0.161537</td>
<td>11.914</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>northern_red.1 - shumard.0 == 0</td>
<td>1.416254</td>
<td>0.162224</td>
<td>8.73</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>nuttall.1 - shumard.0 == 0</td>
<td>1.294502</td>
<td>0.161646</td>
<td>8.008</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>scarlet.1 - shumard.0 == 0</td>
<td>1.425248</td>
<td>0.163265</td>
<td>8.73</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>shumard.1 - shumard.0 == 0</td>
<td>1.688985</td>
<td>0.161703</td>
<td>10.445</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>southern_red.1 - shumard.0 == 0</td>
<td>2.169971</td>
<td>0.1676</td>
<td>12.947</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.1 - shumard.0 == 0</td>
<td>1.405387</td>
<td>0.16999</td>
<td>8.267</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.0 - southern_red.0 == 0</td>
<td>-0.941181</td>
<td>0.15185</td>
<td>-6.198</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>black.1 - southern_red.0 == 0</td>
<td>0.885367</td>
<td>0.154195</td>
<td>5.742</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>cherrybark.1 - southern_red.0 == 0</td>
<td>0.774371</td>
<td>0.151293</td>
<td>5.118</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>northern_red.1 - southern_red.0 == 0</td>
<td>0.266082</td>
<td>0.153221</td>
<td>1.737</td>
<td>0.9345</td>
</tr>
<tr>
<td>nuttall.1 - southern_red.0 == 0</td>
<td>0.144331</td>
<td>0.152934</td>
<td>0.944</td>
<td>0.9999</td>
</tr>
<tr>
<td>scarlet.1 - southern_red.0 == 0</td>
<td>0.275077</td>
<td>0.154302</td>
<td>1.783</td>
<td>0.9198</td>
</tr>
<tr>
<td>shumard.1 - southern_red.0 == 0</td>
<td>0.538814</td>
<td>0.151994</td>
<td>3.545</td>
<td>0.0327</td>
</tr>
<tr>
<td>southern_red.1 - southern_red.0 == 0</td>
<td>1.0198</td>
<td>0.156868</td>
<td>6.501</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.1 - southern_red.0 == 0</td>
<td>0.255216</td>
<td>0.161895</td>
<td>1.576</td>
<td>0.9711</td>
</tr>
<tr>
<td>Model</td>
<td>β</td>
<td>SE</td>
<td>Z</td>
<td>P</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-------</td>
<td>-------</td>
<td>-------</td>
<td>---------</td>
</tr>
<tr>
<td>black.1 - willow.0 == 0</td>
<td>1.826</td>
<td>0.154</td>
<td>11.837</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>cherrybark.1 - willow.0 == 0</td>
<td>1.715</td>
<td>0.150</td>
<td>11.374</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>northern_red.1 - willow.0 == 0</td>
<td>1.207</td>
<td>0.152</td>
<td>7.905</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>nuttall.1 - willow.0 == 0</td>
<td>1.085</td>
<td>0.152</td>
<td>7.132</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>scarlet.1 - willow.0 == 0</td>
<td>1.216</td>
<td>0.153</td>
<td>7.946</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>shumard.1 - willow.0 == 0</td>
<td>1.479</td>
<td>0.152</td>
<td>9.745</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>southern_red.1 - willow.0 == 0</td>
<td>1.960</td>
<td>0.157</td>
<td>12.496</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.1 - willow.0 == 0</td>
<td>1.196</td>
<td>0.158</td>
<td>7.583</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>cherrybark.1 - black.1 == 0</td>
<td>-0.111</td>
<td>0.136</td>
<td>-0.815</td>
<td>0.4482</td>
</tr>
<tr>
<td>northern_red.1 - black.1 == 0</td>
<td>-0.619</td>
<td>0.137</td>
<td>-4.51</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>nuttall.1 - black.1 == 0</td>
<td>-0.741</td>
<td>0.140</td>
<td>-5.289</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>scarlet.1 - black.1 == 0</td>
<td>-0.610</td>
<td>0.137</td>
<td>-4.441</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>shumard.1 - black.1 == 0</td>
<td>-0.346</td>
<td>0.137</td>
<td>-2.522</td>
<td>0.0164</td>
</tr>
<tr>
<td>southern_red.1 - black.1 == 0</td>
<td>0.134</td>
<td>0.140</td>
<td>9.566</td>
<td>0.9999</td>
</tr>
<tr>
<td>willow.1 - black.1 == 0</td>
<td>-0.630</td>
<td>0.145</td>
<td>-4.334</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>northern_red.1 - cherrybark.1 == 0</td>
<td>-0.508</td>
<td>0.135</td>
<td>-3.761</td>
<td>0.0158</td>
</tr>
<tr>
<td>nuttall.1 - cherrybark.1 == 0</td>
<td>-0.630</td>
<td>0.136</td>
<td>-4.621</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>scarlet.1 - cherrybark.1 == 0</td>
<td>-0.499</td>
<td>0.133</td>
<td>-3.738</td>
<td>0.0164</td>
</tr>
<tr>
<td>shumard.1 - cherrybark.1 == 0</td>
<td>-0.236</td>
<td>0.135</td>
<td>-1.751</td>
<td>0.9301</td>
</tr>
<tr>
<td>southern_red.1 - cherrybark.1 == 0</td>
<td>0.245</td>
<td>0.137</td>
<td>1.779</td>
<td>0.9217</td>
</tr>
<tr>
<td>willow.1 - cherrybark.1 == 0</td>
<td>-0.519</td>
<td>0.140</td>
<td>-3.69</td>
<td>0.0201</td>
</tr>
<tr>
<td>nuttall.1 - northern_red.1 == 0</td>
<td>-0.122</td>
<td>0.135</td>
<td>-0.901</td>
<td>0.9999</td>
</tr>
<tr>
<td>scarlet.1 - northern_red.1 == 0</td>
<td>0.009</td>
<td>0.129</td>
<td>0.069</td>
<td>1</td>
</tr>
<tr>
<td>shumard.1 - northern_red.1 == 0</td>
<td>0.273</td>
<td>0.133</td>
<td>2.05</td>
<td>0.7905</td>
</tr>
<tr>
<td>southern_red.1 - northern_red.1 == 0</td>
<td>0.754</td>
<td>0.140</td>
<td>5.356</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.1 - northern_red.1 == 0</td>
<td>-0.010</td>
<td>0.145</td>
<td>-0.075</td>
<td>0.9998</td>
</tr>
<tr>
<td>scarlet.1 - nuttall.1 == 0</td>
<td>0.131</td>
<td>0.133</td>
<td>0.983</td>
<td>0.9998</td>
</tr>
<tr>
<td>shumard.1 - nuttall.1 == 0</td>
<td>0.394</td>
<td>0.135</td>
<td>2.92</td>
<td>0.0201</td>
</tr>
<tr>
<td>southern_red.1 - nuttall.1 == 0</td>
<td>0.875</td>
<td>0.143</td>
<td>6.135</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.1 - nuttall.1 == 0</td>
<td>0.111</td>
<td>0.143</td>
<td>0.77</td>
<td>1</td>
</tr>
<tr>
<td>shumard.1 - scarlet.1 == 0</td>
<td>0.263</td>
<td>0.133</td>
<td>1.98</td>
<td>0.8313</td>
</tr>
<tr>
<td>southern_red.1 - scarlet.1 == 0</td>
<td>0.745</td>
<td>0.139</td>
<td>5.346</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>willow.1 - scarlet.1 == 0</td>
<td>-0.019</td>
<td>0.141</td>
<td>-0.141</td>
<td>0.8407</td>
</tr>
<tr>
<td>southern_red.1 - shumard.1 == 0</td>
<td>0.480</td>
<td>0.140</td>
<td>3.426</td>
<td>0.0494</td>
</tr>
<tr>
<td>willow.1 - shumard.1 == 0</td>
<td>-0.284</td>
<td>0.144</td>
<td>-1.964</td>
<td>0.8407</td>
</tr>
<tr>
<td>willow.1 - southern_red.1 == 0</td>
<td>-0.765</td>
<td>0.147</td>
<td>-5.209</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>
Coefficient estimates with 95% confidence intervals for significant variables in the top ranked Cox mixed regression model. Treatment significantly increased the probability of acorn removal in control plots (Coeff. = 2.818, p < 0.01). Caching predator presence had a significant interaction with treatment that decreased the treatment effect (Coeff. = -0.844, p < 0.01). Non-caching predator presence had a significant interaction with treatment that decreased the treatment effect (Coeff. = -1.908, p < 0.01).
Table A.2  Coefficient estimates from second highest ranked model.

<table>
<thead>
<tr>
<th></th>
<th>Coeff</th>
<th>Exp(coeff)</th>
<th>SE(coef)</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>treatment_control</td>
<td>2.818</td>
<td>16.745</td>
<td>0.571</td>
<td>4.930</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Non-caching-pred</td>
<td>1.394</td>
<td>4.030</td>
<td>0.105</td>
<td>13.220</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>acorn_spp_cherrybark</td>
<td>-0.361</td>
<td>0.697</td>
<td>0.152</td>
<td>-2.370</td>
<td>0.018</td>
</tr>
<tr>
<td>acorn_spp_northern_red</td>
<td>-0.614</td>
<td>0.541</td>
<td>0.157</td>
<td>-3.910</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>acorn_spp_nuttall</td>
<td>-1.347</td>
<td>0.260</td>
<td>0.161</td>
<td>-8.360</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>acorn_spp_scarlet</td>
<td>-0.583</td>
<td>0.558</td>
<td>0.156</td>
<td>-3.730</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>acorn_spp_nuttall</td>
<td>-1.066</td>
<td>0.344</td>
<td>0.158</td>
<td>-6.770</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>acorn_spp_southern_red</td>
<td>0.198</td>
<td>1.218</td>
<td>0.144</td>
<td>1.370</td>
<td>0.170</td>
</tr>
<tr>
<td>acorn_spp_willow</td>
<td>-0.772</td>
<td>0.462</td>
<td>0.155</td>
<td>-4.990</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Caching-pred</td>
<td>1.520</td>
<td>4.572</td>
<td>0.171</td>
<td>8.900</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>property_strawberry_plains</td>
<td>-0.254</td>
<td>0.776</td>
<td>0.553</td>
<td>-0.460</td>
<td>0.650</td>
</tr>
<tr>
<td>Treatment_control*non-caching-pred</td>
<td>-1.908</td>
<td>0.148</td>
<td>0.189</td>
<td>-10.090</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>acorn_spp_cherrybark*caching-pred</td>
<td>0.221</td>
<td>1.247</td>
<td>0.204</td>
<td>1.080</td>
<td>0.280</td>
</tr>
<tr>
<td>acorn_spp_northern_red*caching-pred</td>
<td>-0.029</td>
<td>0.971</td>
<td>0.208</td>
<td>-0.140</td>
<td>0.890</td>
</tr>
<tr>
<td>acorn_spp_nuttall*caching-pred</td>
<td>0.593</td>
<td>1.810</td>
<td>0.212</td>
<td>2.800</td>
<td>0.005</td>
</tr>
<tr>
<td>acorn_spp_scarlet*caching-pred</td>
<td>-0.080</td>
<td>0.923</td>
<td>0.207</td>
<td>-0.390</td>
<td>0.700</td>
</tr>
<tr>
<td>acorn_spp_shumard*caching-pred</td>
<td>0.718</td>
<td>2.051</td>
<td>0.209</td>
<td>3.440</td>
<td>0.001</td>
</tr>
<tr>
<td>acorn_spp_southern_red*caching-pred</td>
<td>-0.061</td>
<td>0.941</td>
<td>0.201</td>
<td>-0.300</td>
<td>0.760</td>
</tr>
<tr>
<td>acorn_spp_willow*caching-pred</td>
<td>0.104</td>
<td>1.109</td>
<td>0.209</td>
<td>0.500</td>
<td>0.620</td>
</tr>
<tr>
<td>treatment_control*caching-pred</td>
<td>-0.845</td>
<td>0.430</td>
<td>0.179</td>
<td>-4.720</td>
<td>&lt;.001</td>
</tr>
</tbody>
</table>