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IN THE PINES: DUNG BEETLE COMMUNITY COMPOSITION
IN LONGLEAF PINE HABITAT

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Forest Resources

by
Kelsea Lynn Young
December 2021

Accepted by:
Dr. Jessica Hartshorn, Committee Chair
Dr. Kier Klepzig
Dr. Michael Caterino

ABSTRACT

Dung beetle assemblages are recognized as ecological bioindicators, allowing us to monitor ecological impacts by observing community shifts. Acting as primary nutrient cyclers, they establish niche segregation by sometimes selecting dung based on species (e.g., coyote vs. deer) and by using dung in different ways (e.g., rollers vs. tunnelers). Longleaf pine savannahs are recognized as global hotspots for diversity. Species of dung beetles found within these ecosystems may differ substantially from those found in surrounding agricultural, residential or other forest land. Our objective was to investigate whether the exclusion of mammalian meso-predator exclusion impacts dung beetle abundance, species composition and community diversity within a pristine longleaf pine forest. We randomized dung pitfall traps along a single transect inside four predator exclusion plots and in paired open control plots, each approximately 40.5 hectares in size, in longleaf pine forests at The Jones Center at Ichauway, a nature preserve and research center in southwest Georgia. We collected from traps 72 hours after baits were placed each month, over a two-year period. We identified dung beetles to species or genus level excluding aphodiines which we identified to the subfamily level.

We compared species composition, population densities, and associated diversity indices between predator exclusion and control (non-exclusion) plots. The exclusion of predators affected the abundance and composition of individual species, while whole

communities were affected by individual sites. When we controlled for seasonality, we found significant differences in species diversity between sites with predators and those without.

DEDICATION

This thesis is dedicated to my spouse, Jeffrey Alan Young, who has continuously encouraged, challenged, and lifted me up whenever I was down. Thank you for your tolerance of drawers full of beetles scattered throughout our home and cars full of dung coolers continuously transported across multiple state lines. You have been on this journey with me every step along the way and my love and gratitude cannot adequately be put into words.

ACKNOWLEDGMENTS

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To my dear lab mates, we were on a tumultuous journey together and I couldn't ask for better partners to share the experience with. Thank you to my best friend, Katy Crout, for always taking time to listen and offering ice cream and sweet tea whenever I became overwhelmed. A very special thank you belongs to my therapist, Dr. Chris Ruth, for aiding in my efforts to stay sane and accountable throughout this process. Lastly, I thank my spouse for continuously being my rock of steadfast reassurance and encouragement.

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CHAPTER ONE

DUNG BEETLES AND LONGLEAF PINE SYSTEMS

1. Introduction and overview

Ecosystem Services

Ecosystems are considered “any unit that includes all the organisms (i.e. the community) in a given area interacting with the physical environment so that the flow of energy leads to clearly defined trophic structure, biotic diversity and material cycles (i.e. exchange of materials between living and non-living parts) within the system” (Odum and Barrett 1971). With this project, I aimed to examine if the removal of mammalian meso-predators impacts key insect players that perform the function of removing dung from the ecosystem. Many organisms, including insects, recycle nutrients through the process of dying, and by decomposing organic matter, thereby converting nutrients from organic to their inorganic form that can be used by other organisms (DeAngelis 2012). Common nutrient cyclers include saproxylic insects, earthworms, fungi, dung beetles, and carrion beetles (Nichols et al. 2007, Weisser and Siemann 2008).

Dung beetles are efficient nutrient cyclers that provide a variety of functional roles within their respective ecosystems (Nichols et al. 2007), and are found in most ecosystems where they are adapted to handle dung. Changes to these ecosystems can slow the process of nutrient cycling and lead to the accumulation of dung, as is the case with the importation of non-native livestock. In those cases, specialist dung beetles have been imported to deal with the overabundance of livestock dung, as in Australia, and the southeastern United States (Doube 2018, Young 2007). In addition to nutrient cycling,

dung beetles serve in a variety of other ecological roles including seed dispersal, bioturbation (the disturbance of sedimentary material), and pollination (Nichols et al. 2007). Dung beetles speed up the nutrient cycling process and soil turnover rates using vertebrate dung, fungi, and occasionally carrion.

Dung beetles provide a variety of other ecosystem functions that are less commonly attributed to them. Beneficial scarabaeoid dung beetles [Geotrupidae (Geotrupinae) and Scarabaeidae (Aphodiinae), Coprinae, and Scarabaeinae)] compete for nesting and food resources with dung-breeding Diptera, reducing the survival rate of dipterans and the survival of dung born intestinal parasites including helminths and *Cryptosporidium* (Bertone et al. 2005, Doube 2018, Bryan 1973, Fincher 1973). Dung beetles reduce instances of human-pathogenic *Escherichia coli* on food-crops as well as reduce the numbers of calliphorid flies which spread *E. coli* (Jones et al. 2019). Many dung beetles participate in secondary seed dispersion by burying dung of frugivorous vertebrates, providing refugia from seed predators and aiding in forest regeneration (Vinod and Sabu 2007, Vulinec 2002). Survival rates for seeds are higher in dung that has been buried compared to dung remaining on the soil surface (Santos-Heredia et al. 2010, Andresen and Feer 2005). Lastly, a less commonly attributed function for dung beetles is that of pollinators for dung and carrion scented flowers such as *Dracunculus* and *Sauromatum* (Araceae) and *Orchidantha inouei* (Lowiaceae) pollinated primarily by *Onthophagus* spp. scarabaeid beetles (Meeuse and Hatch 1960, Sakai and Inoue 1999).

Biological Indicators

Dung beetles are abundant in the southeastern United States and respond to habitat heterogeneity at local scales. They can be very specialized, provide myriad ecosystem services, and have well defined ecological roles. These factors combine to make them excellent biological indicators (organisms whose presence and/or abundance reveal certain characteristics about the environment), especially of biodiversity (Spector 2006, Halfpeter and Favila 1993, Nichols et al. 2007, Gardner et al. 2008, Cambefort and Hanski 1991). They are susceptible to a variety of conservation threats, especially due to shifts in land use (Nichols et al. 2007). In forested systems, they are considered good indicators of both human and large herbivore caused landscape shifts (Vinod and Sabu 2007). However, while invertebrates are often significantly impacted by shifts in land use, they are often overlooked in studies focused on disturbance (Nichols et al. 2007). In one study by Bertone et al. (2005) the vast majority (95%) of coprophagous species trapped in pastureland was comprised of nine exotic species, indicating that pastureland is dominated by exotics in comparison to forests which are largely dominated by native species.

2. Biology and niche partitioning

Beetles (Coleoptera) are the largest order in class Insecta with approximately 400,000 species. The dung beetle guild is highly diverse with thousands of species across multiple families, many of which have not been thoroughly studied. Most dung beetle species are dependent upon vertebrate excrement to complete their life cycle (Byk and Piętko 2018). Through their utilization of excrement, they return essential nutrients to the ecosystem.

Niche partitioning has evolved due to competition for shared resources, unsurprisingly, dung associated beetles participate in spatial and temporal niche segregation (Bertone et al. 2005, Young 2007). Dung beetles are divided biologically and taxonomically into three behavioral/ spatial niches: dung dwellers (endocoprids), dung tunnelers (paracoprids), and dung rollers (telecoprids). Each utilize their own unique method for harvesting and utilizing vertebrate excrement. Endocoprid species reside within the dung pat, laying eggs directly in the dung while paracoprids form tunnels beneath the dung pat that lead to brooding chambers where they lay eggs on dung stores. Telecoprids are what most people commonly associate with dung beetles, as they roll portions or balls of the dung away from the original dung pat to separate tunneled brooding chambers (Byk and Piętko 2018).

Endocoprids in the Eastern US are often classified as either “forest dwellers” or “field dwellers”, the latter of which are typically associated with agrarian landscapes. Forest dwelling communities are composed primarily of native species such as *Onthophagus concinnus* and *Onthophagus hecate*, while field dwelling species are often composed of introduced species such as *Digitonthophagus gazelle* and *Onthophagus taurus*, which are species better equipped to handle large dung pats of introduced livestock. The window of efficacy (the time period in which dung remains attractive to dung beetles for trapping) for trapping remains poorly understood. However anecdotally, has been observed to have some impact on dung beetle assemblages (pers. obs.). Often telecoprids are the first to arrive at fresh dung pats, molding the pliable excrement into balls to roll away from competing insects (Byk and Piętko 2018). Some unique species

are even adapted to dwell on their target vertebrates, waiting for dung to be deposited so they can quickly utilize and consume the fresh excrement (Matthews 1972, Byk and Piętko 2018). Dung beetles are known to have some preference for dung type and significant differences have been found among omnivore, herbivore, and carnivore dung (Whipple and Hoback 2012). However, preference for the specific bait type is seemingly not correlated with dung quality, mammalian diet, nor origin of mammal (Whipple and Hoback 2012). They are also known to show seasonal separation, with interspecies interactions declining in winter months (Bertone et al. 2005, Young 2007).

3. Study System

Longleaf Systems

Longleaf pine woodlands can be defined, in part, by extremely diverse understory growth which is dependent on short fire regimes and myriad microhabitats positioned within the ecosystem (Peet 2006). Many unique plant and animal species are associated with this ecosystem, including the gopher tortoise (*Gopherus polyphemus*) which acts as a keystone species to dozens of other animals that share its burrows. The red-cockaded woodpecker (*Leuconotopicus borealis*) is another species dependent on longleaf pine and is federally endangered (Engstrom and Sanders 1997, Engstrom 1993). Many mammal species also thrive in longleaf forests including southeastern fox squirrel (*Sciurus niger*), southeastern pocket gopher (*Geomys pinetis*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), and white-tailed deer (*Odocoileus virginianus*) (Engstrom 1993). This diverse and unique ecosystem has declined dramatically over the past two-hundred years due to

changes in land-use with less than 5% of the original coverage by fire-maintained natural longleaf forests remaining (Jose et al. 2006, Means and Grow 1985).

Human impacts to longleaf pine forests, including habitat fragmentation from deforestation, expansion of agriculture and cattle ranching, and urbanization play a key role in shaping extant dung and carrion beetle communities but most research thus far has been in agrarian or tropical systems. Overall, little is known about the effects of landscape fragmentation on forest insect communities (Diaz et al. 2010) or about arthropod communities in longleaf pine habitat (Folkerts et al. 1993, Sheehan and Klepzig 2021). However, there is some evidence for the impacts of land use changes on dung and carrion beetle assemblages. For example, in the tropics, it was found that secondary forests, agroforests, and selectively logged forests supported rich insect communities with many forest-dwelling species while clear-cuts and cattle pastures contained fewer overall species and few forest-dwelling species (Nichols et al. 2007).

My study location was the Jones Center at Ichauway, a 11,735-hectare research center that is essentially as an “ecological island” of vast fire-managed longleaf pine forest surrounded by center-pivot irrigated agrarian systems and fragmented commercial forests that could be impacted by land use changes in the surrounding landscapes (Figure 1.1). My study sites are located in the northern portion of the property and consist of four mammalian-predator exclusion plots and four paired controls. These sites were established to examine the effects of mesopredators on common prey in the longleaf pine ecosystem (Conner et al. 2011). The sites are primarily longleaf pine but are composed of a variety of microhabitats including young and mature longleaf pine stands, mixed pine-

hardwood stands, and wetlands. Each predator exclusion site and paired control are of similar habitat type, though some variation occurs.

Multi-trophic interactions

Insects are abundant and diverse in most habitats, functioning as key players in various ecosystem processes, the loss of which can result in negative cascading effects throughout entire communities (Coleman and Hendrix 2000). Alterations to decomposers, such as dung beetle communities, may have easily observable trophic effects. For example, in Australia the introduction of non-native livestock without their associated dung beetles resulted in a massive accumulation of dung. Native Australian dung beetles which had evolved to handle small and hard marsupial dung were ill equipped to manage the dung of large mammals (Doube 2018). As a result, populations of dung-breeding bush flies (*Musca vetustissima*), a nuisance fly and disease vector, exploded (Sutton 1933).. Following the introduction of 53 exotic dung beetle species in Australia by CSIRO (Commonwealth Scientific and Industrial Research Organization), 23 of which have become established, the problem of an overabundance of livestock dung in Australia was mitigated (Doube 2018). Dependence on vertebrate dung makes it plausible that dung beetle communities are likely to be impacted by shifts in mammal communities (Estrada et al. 1999).

4. Objectives

As their value as bioindicators has been acknowledged over recent years, research on dung beetles has surged (Spector 2006, Nichols et al. 2007, Scholtz 2012, Davis et al.

2001). Still, studies of dung beetles in temperate, non-agricultural habitats remain limited (Davis and Scholtz 2004, Barragán et al. 2011). Even fewer studies exist looking at insect communities in longleaf pine forests. The effects of removing mammalian meso-predators on invertebrate communities has also not been well noted, particularly in reference to nutrient cycling processes. We used mammal dung from predators (coyote and bobcat), and a prey species, whitetail deer. The dung from these larger mammals provides a food resource for dung species. Dung beetles are shown to have a preference for different types of dung (Bogoni and Hernández 2014, Whipple and Hoback 2012, Santos-Heredia et al. 2010) so it seemed likely that removal of these predators could affect dung beetle communities. To address these gaps in knowledge, I explored impacts mammalian meso-predator exclusion by comparing dung beetle community composition in longleaf pine habitats, with and without mammalian meso-predators.

The overall goal of this study is to determine the impact of the removal of mammalian meso-predators on dung beetle presence and abundance. To achieve this goal, our study had several objectives: Objective 1) Determining the species composition, population densities, and diversity of dung beetles in a fire managed longleaf pine ecosystem; Objective 2) Observing effects of exclusion of mammalian meso-predators on dung beetle communities. I hypothesized that species richness of dung beetles will be lower where meso-predators have been excluded.

CHAPTER TWO

STUDY DESIGN, RESULTS, AND DISCUSSION

Experimental Design

In 2003, the Jones Center at Ichauway established four meso-predator enclosure areas to examine the impacts of exclusion of meso-predators on various potential prey species including hispid cotton rats and avian nests (Conner et al. 2001). The enclosure sites are kept predator-free by 1.2 m tall woven wire fencing reinforced with three electrified lines of fencing. Exclosures range in size from 35.94 ha to 49.09 ha with a range of habitat types, dominated by longleaf (e.g., wetland, mesic upland). Each enclosure has a paired control of similar size and habitat type (Figure 2.1) which will be referred to henceforth as “sites”. Exclosure sites are further kept predator-free by thermal camera surveys and track counts coupled with live trapping of predators. Although mammalian meso-predators occasionally enter enclosure areas, monitoring suggests that these areas have significantly fewer mammalian meso-predators (Conner et al. 2010).

Each enclosure and paired control site contains pre-established small mammal trapping grids consisting of 144 marked survey points in a 12-point \times 12-point grid, with each point being 15 m apart. Within each grid, we placed six, randomly baited dung traps along a diagonal transect, bisecting the grid, with \sim 42.4 m spacing between each trap. Dung traps contained captive deer (positive control), coyote, or bobcat dung (supplied by the Western North Carolina Nature Center, Asheville, NC; WildWNC.org). Dung traps were placed once a month and collected \sim 72 hours later between June 2019 through June 2021.

Trap Design

We collected beetles by way of modified dung-baited pitfall traps. Dung pitfall traps consisted of a 473 mL deli cup (11.4 cm dia.), inserted into a 946 mL deli cup. We removed the rim of the smaller cup such that the smaller cup could sit flush against the larger cup, which was placed flush to the ground. We filled a 29.6 mL cup with dung and a solution of water and liquid soap and suspended over the smaller deli cup with a wire loop. Covers consisted of a 15.2 × 15.2 cm plastic roofing shim, secured to the ground with 15.2 cm staples (Figure 2.2).

While we sorted and identified all beetles from the dung traps, we focused on taxa within the decomposer guild. We saved other orders at The Jones Center at Ichuaway for future study.

Statistical Analyses

We collected samples over a period of twenty-four months between June 2019 and June 2021, excluding January 2020 (sample mishandled), and April and October 2020 (inability to collect due to COVID-19 restrictions).

To identify the effects of predator exclusion, site, and bait on dung beetles, I conducted a multivariate analysis of covariance (MANCOVA) on each species collected. I then conducted a permutational analysis of variance (PERMANOVA) to determine differences between communities with regards to site and predator exclusion. I then created a generalized linear model (GLM) to determine if Shannon diversity indices were significantly affected by predator exclusion and site. Finally, I conducted a paired t-test to

investigate the effect of site type (control vs. enclosure) on community diversity to control for seasonality and site. All statistics were performed in R (R Core Team 2020).

Results

The most common dung beetle collected was *Melanocanthon bispinatus* with a total of 5648 individuals (49.6%), comprising of nearly half of all beetles collected (n=11,734). The least common beetles collected were a singleton of *Bradycinetulus ferrugineus*, and tripletons of *Dichotomius carolinus* and *Omorgus* sp. Control plots had a total of 4,888 dung beetles while enclosure plots had a total of 6,846 dung beetles.

There were significant differences in species composition among site type (enclosure vs. control) ($F=3.0760$, $df=1$, $p\text{-value}<0.0001$) and site ($F=2.544$, $df=3$, $p\text{-value}<0.0001$), but not among different types of bait ($F=1.2147$, $df=3$, $p\text{-value}=0.1161$). Because bait was not considered significant, data were combined for bait within each site and site type. Whole communities were significantly affected by site ($F=4.0176$, $df = 3$, $p\text{-value}=0.001$) but not by site type ($F=2.1940$, $df=1$, $p\text{-value}=0.103$).

There were no significant differences among sites or site type when comparing Shannon indices. However, when controlling for seasonality and site with a paired t-test, there were significant differences in Shannon indices between control and enclosure plots ($p\text{-value}=0.0086$) with enclosure plots (1.068 ± 0.061) having higher Shannon indices on average compared to control plots (0.918 ± 0.063).

I also produced a list of collected dung-associated beetles from three families (Scarabaeidae, Geotrupidae, and Trogidae) to a species or genus level, excluding aphodiines which were left at the subfamily level for future expert identification (Table 2.3). Some specialist species, such as the gopher tortoise commensalist *Onthophagus polyphemi* are thought to be present within this ecosystem but require specialized trapping methods for capture. All other beetles were collected and preserved for future examination including staphylinids, carabids, and various other beetle families. These families may have been attracted to dung or were simply captured due to the pitfall design.

Discussion

Surprisingly, Dung beetle abundance and diversity were higher in plots without mesopredators, despite the reduced amount of dung from fewer species (predators and others for which the fences were a barrier) and we found more diverse assemblages of dung beetles within exclosures. While this may be related to the increased abundance of deer dung within exclosures (Cherry et al. 2015, Conner et al. 2016) further exploration of this finding might be advisable. While the dung beetle species we trapped did not show a preference for deer dung, simply having more dung at their disposal may have encouraged an aggregation of dung beetles to these exclosure sites.

Individual species and whole communities responded differently to sites and site type, with individual species showing significant variation, but communities as a whole

showing less variation. This may be due to generalist species replacing the ecological role of specialists when presented with less favorable conditions within sites and site types. Potential unfavorable conditions could be faster desiccation due to soil composition and overstory cover, moisture retention in the soil, and abundance and availability of host species. Specialists may closely follow the hosts life cycle, and thus be congregated in sites and site types that favor the host.

Individual species were affected by site and site type but not bait type, indicating that more generalists exist in these communities. When examining whole communities, they were shown to not be affected by site type, but they were affected by site. While each site is located within a similar habitat on the same property, variations exist in the longleaf pine habitat at Ichauway including tree density and age, understory species composition, the presence of water sources such as ephemeral wetlands, soil composition and variable presence of hardwood species. We were unable to ascertain which specific variables had the greatest impact on dung beetle communities and this area remains open for further study.

Seasonality also added variation in species composition and abundance, so it follows that seasonality can play a role in observed communities, altering community composition and structure. Controlling for this seasonality and site showed that significant differences exist between the control and exclosure plots regarding species diversity. Shannon indices were not significantly related to type, until seasonality was controlled for.

Some of the challenges and limitations of this study include the large variety of microhabitats within the ecosystem, which leads to higher biodiversity, making it difficult to fully account for the site differences within The Jones Center without higher replication of sites and plots. We also missed two months of collection data as a result of COVID-19 and one month due to sample mishandling. Trap design could also be improved upon with sourcing stronger materials for trap roofs or replacing them mid-study as the shims used began to become brittle in the sun after approximately a year and a half use. Mixing dung samples with water to increase moisture content before baiting the traps could also potentially extend the efficacy of dung attraction as the extreme summer heat sometimes evaporated all moisture within the dung bait. Spacing of individual traps could be expanded to reduce the risk of attraction overlap between individual traps. Trapping seasonally or bi-monthly instead of monthly for a two-year study would also reduce the number of overall beetles collected, allowing for more time for identification.

Possible future directions following this study could include expanding upon our concurrent carrion insect study to explore carrion beetle community composition in longleaf habitat and examine the effects of predator removal on this guild of insects. Examining other nutrient cyclers may provide a clearer picture of how invertebrate communities are impacted when vertebrate meso-predators are removed. Another area for potential exploration is examining dung beetle communities in forested longleaf pine habitat to dung beetle communities in surrounding agrarian systems, which often show introduced species among the most abundant (Kaufman and Wood 2012).

Other logical next steps would include increasing the granularity of the study by exploring the effects of dung preference, site type, and specific site on individual species in order to identify which species are generalists and which are specialists within the community. Including introduced bovine dung such as cattle may allow us to detect introduced species at the sites. Further, exploring site differences such as wetlands vs. pine stands vs. mixed hardwood stands would allow for further explanation of site differences. Examining specific sites with individual species would allow the identification of which species are generalists and which are specialists within the community. This study provides another example of the complex interactions among abundant and diverse fauna which are commonplace in this global hotspot for biodiversity. Though we have developed some insights into this decomposer system in this longleaf pine ecosystem. However much remains to be discovered and may be essential to its restoration of longleaf pine woodlands to the broader, fragmented landscape

APPENDICES

Appendix A: Dung Beetle Location, Trap Design, and Results

Chapter 1 Figures

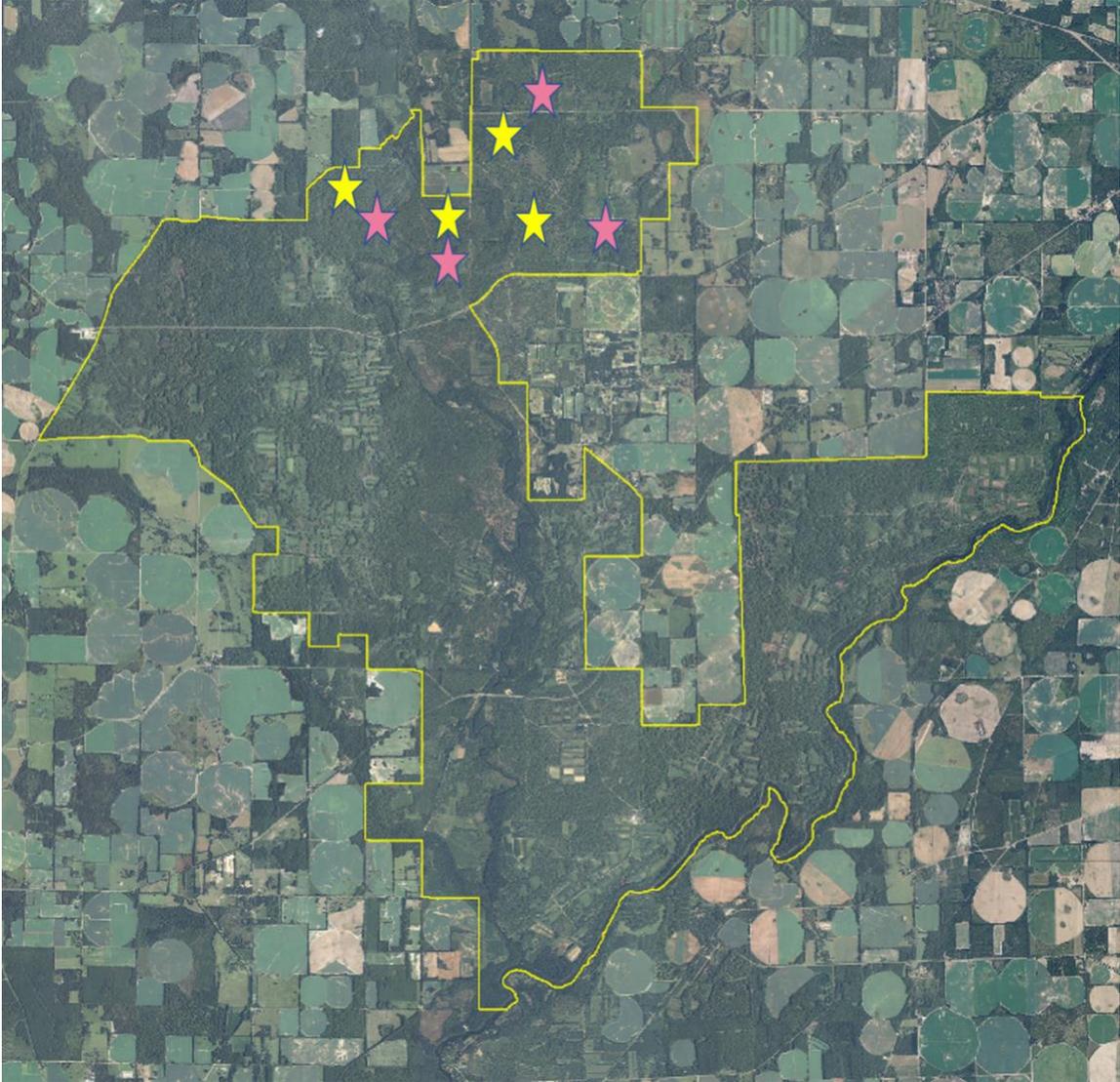


Figure 1.1: Aerial map of Ichauway, with starred study sites (Yellow=control, Pink=exclosure) occurring in the northern portion of the property.

Chapter 2 Figures

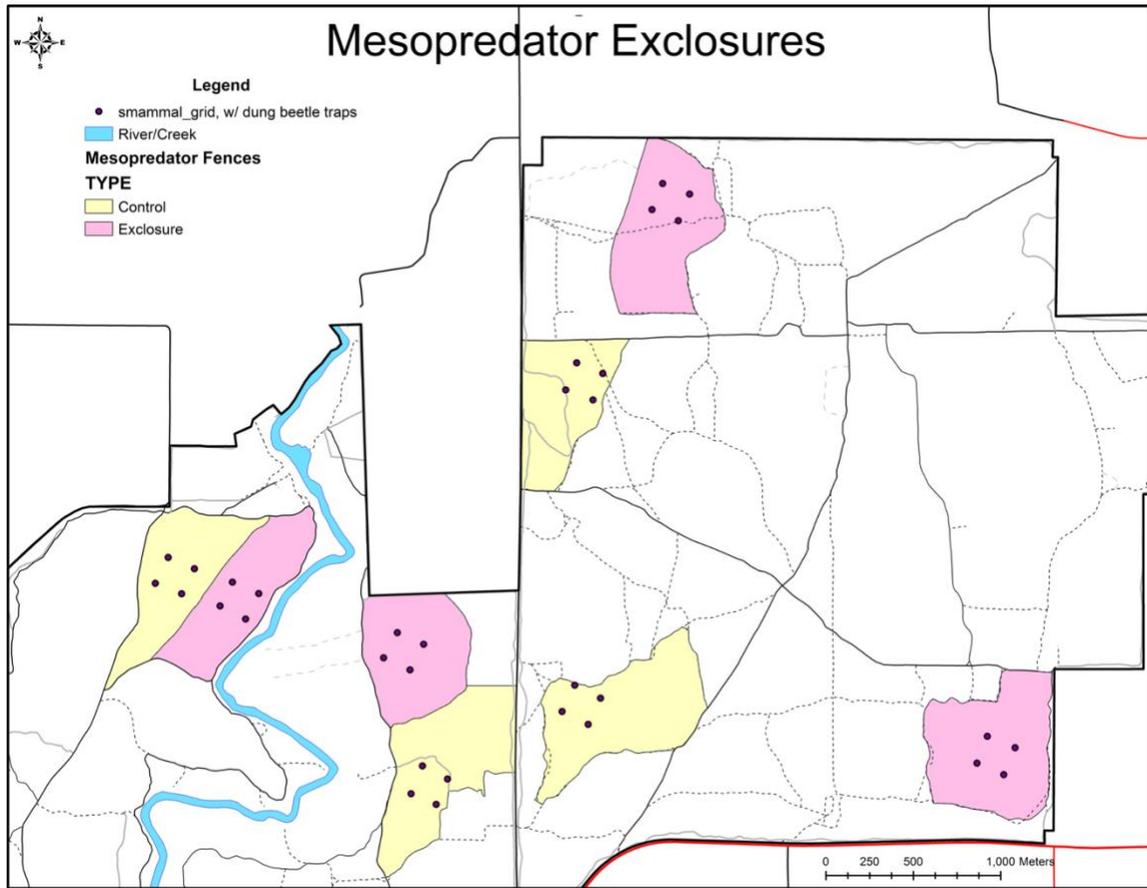


Figure 2.1: GIS map of paired exclosure and control plots and the small mammal grids within them. Traps were placed in a transect across the established small mammal grids.



Figure 2.2: Dung beetle trap design

	Dam Woods		George Creek		Green Grove		Holt Pond	
	Control	Exclosure	Control	Exclosure	Control	Exclosure	Control	Exclosure
<i>Melanocanthon bispinatus</i>	223	371	1037	926	572	865	797	857
<i>Onthophagus tuberculifrons</i>	254	101	34	60	87	548	52	279
<i>Onthophagus concinnus</i>	205	114	64	89	56	114	49	54
<i>Ateuchus</i> sp.	0	0	0	0	0	316	6	391
<i>Copris minutus</i>	80	67	154	181	76	23	74	51
<i>Mycotrupes cartwrighti</i>	33	137	61	78	72	20	9	125
<i>Canthon vigilans</i>	8	81	66	54	72	15	10	40
<i>Trox</i> sp.	23	21	41	99	35	32	15	28
<i>Onthophagus pennsylvanicus</i>	32	51	56	12	36	14	14	22
<i>Phanaeus igneus</i>	4	22	12	96	9	50	7	16
<i>Phanaeus vindex</i>	21	70	16	11	28	42	4	9
<i>Canthon depressipennis</i>	11	7	5	15	71	25	5	0
Aphodiinae	27	33	8	7	24	13	7	17
<i>Geotrupes</i> sp.	7	12	11	11	9	25	9	24
<i>Onthophagus striatulus</i>	20	8	24	13	10	6	1	9
<i>Onthophagus hecate</i>	8	7	41	4	22	4	3	1
<i>Deltochilum gibbosum</i>	1	8	13	3	3	16	8	5
<i>Onthophagus oklahomensis</i>	4	8	16	2	4	2	6	6
<i>Pseudocanthon perplexus</i>	4	0	0	0	0	0	0	0
<i>Dichotomius carolinus</i>	0	2	0	0	0	1	0	0
<i>Omorgus</i> sp.	1	0	2	0	0	0	0	0

<i>Bradycinetulus ferrugineus</i>	0	0	0	0	0	1	0	0
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Figure 2.3: Total individual beetle count

REFERENCES

- Andresen, E., and F. Feer. 2005. The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. Seed fate: Predation, dispersal and seedling establishment :331-349.
- Barragán, F., C. E. Moreno, F. Escobar, G. Halffter, and D. Navarrete. 2011. Negative impacts of human land use on dung beetle functional diversity. PloS one 6:e17976.
- Bertone, M., J. Green, S. Washburn, M. Poore, and C. Sorenson. 2005. Seasonal Activity and Species Composition of Dung Beetles (Coleoptera: Scarabaeidae and Geotrupidae) Inhabiting Cattle Pastures in North Carolina. Annals of the Entomological Society of America 98:309-321.
- Bogoni, J. A., and M. I. M. Hernández. 2014. Attractiveness of Native Mammal's Feces of Different Trophic Guilds to Dung Beetles (Coleoptera: Scarabaeinae). Journal of Insect Science 14:.
- Bryan, R. P. 1973. The effects of dung beetle activity on the numbers of parasitic gastrointestinal helminth larvae recovered from pasture samples. Crop & Pasture Science 24:161-168.
- Byk, A., and J. Piętka. 2018. Dung beetles and their role in the nature. Edukacja Biologiczna i Środowiskowa :17-26.
- Cambefort, Y., and I. Hanski. 1991. Dung beetle population biology. Dung beetle ecology 1:36-50.
- Catling, P. M. 2001. Extinction and the importance of history and dependence in conservation. Biodiversity 2:2-14.
- Michael J. Cherry, L. Mike Conner, Robert J. Warren, 2015. Effects of predation risk and group dynamics on white-tailed deer foraging behavior in a longleaf pine savanna, Behavioral Ecology, Volume 26, Issue 4, Pages 1091–1099.
- Coleman, D. C., and P. F. Hendrix. 2000. Invertebrates as webmasters in ecosystems. CABI, .
- Conner, L. Mike, Steven B. Castleberry, and Anna M. Derrick. 2011. Effects of mesopredators and prescribed fire on hispid cotton rat survival and cause-specific mortality. The Journal of Wildlife Management 75.4 : 938-944.

- Conner, L.M., Cherry, M.J., Rutledge, B.T., Killmaster, C.H., Morris, G. and Smith, L.L. 2016. Predator exclusion as a management option for increasing white-tailed deer recruitment. *Journal of Wildlife Management* 80:162-170
- Crowson, R. A. 2013. *The biology of the Coleoptera*. Academic press.
- Davis, A. L., and C. H. Scholtz. 2004. Local and regional species ranges of a dung beetle assemblage from the semi-arid Karoo/Kalahari margins, South Africa. *Journal of Arid Environments* 57:61-85.
- Davis, A. J., J. D. Holloway, H. Huijbregts, J. Krikken, A. H. Kirk-Spriggs, and S. L. Sutton. 2001. Dung Beetles as Indicators of Change in the Forests of Northern Borneo. *Journal of Applied Ecology* 38:593-616.
- DeAngelis, D. L. 2012. *Dynamics of nutrient cycling and food webs*. Springer Science & Business Media.
- Diaz, A., E. Galante, and M. E. Favila. 2010. The Effect of the Landscape Matrix on the Distribution of Dung and Carrion Beetles in a Fragmented Tropical Rain Forest. *Journal of Insect Science* 10:1-16.
- Doube, B. M. 2018. Ecosystem services provided by dung beetles in Australia. *Basic and Applied Ecology* 26:35-49.
- Engstrom. 1993. *Characteristic Mammals and Birds of Longleaf Pine Forests*. .
- Engstrom, and F. J. Sanders. 1997. Red-Cockaded Woodpecker Foraging Ecology in an Old-Growth Longleaf Pine Forest. *The Wilson bulletin (Wilson Ornithological Society)* 109:203-217.
- Estrada, A., A. Anzures D, and R. Coates-Estrada. 1999. Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*), and dung beetles at Los Tuxtlas, Mexico. *American Journal of Primatology: Official Journal of the American Society of Primatologists* 48:253-262.
- Fincher, T. G. 1973. Dung Beetles as Biological Control Agents for Gastrointestinal Parasites of Livestock. *The Journal of Parasitology* 59:396-399.
- Folkerts, G. W., M. A. Deyrup, and D. C. Sisson. 1993. *Arthropods Associated with Xeric Longleaf Pine Habitats in the Southeastern United States: A Brief Overview*.
- Gardner, T. A., M. I. M. Hernández, J. Barlow, and C. A. Peres. 2008. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *The Journal of applied ecology* 45:883-893.

- Graczyk, T. K., R. Knight, and L. Tamang. 2005. Mechanical Transmission of Human Protozoan Parasites by Insects. *Clinical microbiology reviews* 18:128-132.
- Halfpiter, G., and M. E. Favila. 1993. Halfpiter G, Favila ME. The Scarabaeinae (Insecta: Coleoptera), an animal group for analysing, inventorying and monitoring biodiversity in tropical rainforest and modified landscape... .
- Jones, M. S., S. A. Wright, O. M. Smith, T. E. Besser, D. H. Headrick, J. P. Reganold, D. W. Crowder, and W. E. Snyder. 2019. Organic farms conserve a dung beetle species capable of disrupting fly vectors of foodborne pathogens. *Biological Control* 137:104020.
- Jose, S., E. J. Jokela, and D. L. Miller. 2006. *The Longleaf Pine Ecosystem*. Springer, New York, NY.
- Kaufman, Phillip E., Wood, Lois A. 2012. Indigenous and Exotic Dung Beetles (Coleoptera: Scarabaeidae and Geotrupidae) Collected in Florida Cattle Pastures. *Annals of the Entomological Society of America*, Volume 105, Issue 2, Pages 225–231.
- Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70:1715.
- Kozol, A. J., M. P. Scott, and J. F. A. Traniello. 1988. *The American Burying Beetle, Nicrophorus americanus: Studies on the Natural History of a Declining Species** .
- Lingafelter, S. W. 1995. Diversity, Habitat Preferences, and Seasonality of Kansas Carrion Beetles (Coleoptera: Silphidae). *Journal of the Kansas Entomological Society* 68:214-223.
- Matthews, E. G. 1972. A Revision of the Scarabaeine Dung Beetles of Australia I. Tribe Onthophagini . .
- Means, D. B., and G. Grow. 1985. The endangered longleaf pine community. *Enfo* 85:1-12.
- Meeuse, B. J. D., and M. H. Hatch. 1960. Beetle Pollination in *Dracunculus* and *Sauromatum* (Araceae). *The Coleopterists Bulletin* 14:70-74.
- Nichols, E., T. Larsen, S. Spector, A. L. Davis, F. Escobar, M. Favila, and K. Vulinec. 2007. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. *Biological conservation* 137:1-19.
- Odum, E. P., and G. W. Barrett. 1971. *Fundamentals of ecology*. Saunders Philadelphia, .

- Peet, R. K. 2006. Ecological Classification of Longleaf Pine Woodlands. Pages 51-93 *In* Anonymous The Longleaf Pine Ecosystem, Springer New York, New York, NY.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org>
- Sakai, S., and T. Inoue. 1999. A new pollination system: dung-beetle pollination discovered in *Orchidantha inouei* (Lowiaceae, Zingiberales) in Sarawak, Malaysia. *American Journal of Botany* 86:56-61.
- Santos-Heredia, C., E. Andresen, and D. A. Zárate. 2010. Secondary seed dispersal by dung beetles in a Colombian rain forest: effects of dung type and defecation pattern on seed fate. *Journal of tropical ecology* 26:355-364.
- Scholtz, C. H. 2012. *Evolutionary Biology and Conservation of Dung Beetles*. .
- Scott, M. P. 1998. The Ecology and Behavior of Burying Beetles. *Annual review of entomology* 43:595-618.
- Spector, S. 2006. Scarabaeine Dung Beetles (Coleoptera: Scarabaeidae: Scarabaeinae): An Invertebrate Focal Taxon for Biodiversity Research and Conservation. *Coleopterists Society Monographs. Patricia Vaurie Series* :71-83.
- Sutton, H. 1933. Geographical incidence of disease in Australia. *Australian Geographer* 2:3-10.
- Vinod, K. V., and T. K. Sabu. 2007. Species Composition and Community Structure of Dung Beetles Attracted to Dung of Gaur and Elephant in the Moist Forests of South Western Ghats. *Journal of Insect Science* 7:1-14.
- Vulinec, K. 2002. Dung Beetle Communities and Seed Dispersal in Primary Forest and Disturbed Land in Amazonia. *Biotropica* 34:297-309.
- Watson-Horzelski, E. J., and A. C. Clark-Aguilard. 2011. Predatory Behaviors of *Creophilus maxillosus* (L.) (Coleoptera: Staphylinidae) Towards the Invasive Blow Fly *Chrysomya rufifacies* (Macquart) (Diptera: Calliphoridae). *The Coleopterists Bulletin* 65:177-181.
- Weisser, W. W., and E. Siemann. 2008. *The Various Effects of Insects on Ecosystem Functioning*. Springer Berlin Heidelberg, .
- Whipple, S. D., and W. W. Hoback. 2012. A Comparison of Dung Beetle (Coleoptera: Scarabaeidae) Attraction to Native and Exotic Mammal Dung. *Environmental Entomology* 41:238-244.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat Fragmentation in the Temperate Zone. .:

Young, O. P. 2007. Relationships Between an Introduced and Two Native Dung Beetle Species (Coleoptera: Scarabaeidae) in Georgia. *Southeastern Naturalist* 6:491-504.