
Currently, U.S. state and federal mandates are attempting to lower fossil fuel consumption to reduce dependency on foreign oils and lower greenhouse gas emissions. Intercropping switchgrass \((Panicum virgatum\ L.)\) in southern pine forest is a potential way to grow and harvest a biofuel feedstock without encumbering additional arable land. Rodents are important components of forest ecosystems, and intercropping switchgrass changes the understory vegetation composition and structure, which could influence rodent community structure and population demographics. To examine the sustainability of an intercropping management system, I examined whether intercropping switchgrass in intensively managed loblolly pine \((Pinus taeda)\) plantations affected rodent community structure and population demographics in a large-scale, landscape experiment. Thus, I conducted seven intensive live-trapping sessions June-August 2012 on three intensively managed pine stands (control) and three intensively managed pine stands intercropped with switchgrass. Peromyscus spp. and Sigmodon hispidus were the most common species trapped on both treatment types. Intercropped stands had lower rodent community evenness \((t = 2.79, \text{df} = 4, P = 0.02)\) and diversity \((t = 2.64, \text{df} = 4, P = 0.03)\) than control stands. Sigmodon hispidus abundance was significantly higher \((F_{1,4} = 16.20, P = 0.02)\) in intercropped stands and contributed to over 86% of dissimilarity between treatments while no other species were influenced. However, there was no treatment effect on survival and recruitment. My findings indicate that intercropping switchgrass in managed pine plantations may have altered rodent community diversity by altering evenness and increasing abundance of \(S.\ hispidus\), but not other species in the rodent community. Because \(S.\ hispidus\) is a native rodent which is commonly the most abundant rodent in southeastern pine forests, a
switchgrass intercropping system to produce biofuel feedstock might be a sustainable option for planting switchgrass.
LANDSCAPE-SCALE EFFECTS OF INTERCROPPING SWITCHGRASS 
(PANICUM VIRGATUM L.) AND LOBLOLLY PINE (PINUS TAEDA) 
ON RODENT COMMUNITY STRUCTURE AND 
POPULATION DEMOGRAPHICS

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CHAPTER I
INTRODUCTION

A biofuel is a type of fuel whose energy is derived from biomass (i.e. renewable organic material) [1,2]. Although burning biofuels releases carbon dioxide like fossil fuels, biofuels production uses carbon dioxide and may be a carbon sink [1,2]. United States federal and state mandates require lowering use of fossil fuels to reduce dependency on foreign oils and lower greenhouse gas emissions [3]. Abundant land is required to produce biofuel feedstocks at the scale necessary to meet these mandates [2,3]. First generation biofuels are produced from feedstocks that include row crops, such as corn (Zea mays) or sugarcane (Saccharum spp.), which require high energy input for production [2]. Second generation feedstocks (e.g., agriculture and forestry residues, grasses, and woody material) are potentially a more sustainable biofuel option [2]. When conversion of arable or undisturbed lands, alteration of biodiversity, and reduction of carbon sequestration through deforestation occurs, the sustainability of biofuels production is debatable [1,4–6].

Intercropping of biofuel feedstock crops in managed forests is a potential way to reduce use of fossil fuels and produce carbon neutral, cellulosic energy sources without converting land from another use [7,8]. Switchgrass (Panicum virgatum) has long been considered a promising biofuel feedstock, because it is native to most of eastern North America, grows in a wide variety of ecosystems, has an extensive root system that
stabilizes soil, and may provide carbon storage [2,9–12]. Changing land use from row crops (e.g., corn) to perennial grasses (e.g., switchgrass) has been shown to provide habitat for native grassland bird species [1,5]. Further, switchgrass can be intercropped in pine plantations, which removes the “fuel versus food” debate that has hampered other potential feedstocks, such as corn [2,6,13].

To evaluate ecological sustainability of intercropping switchgrass in pine plantations, it is important to understand how incorporating switchgrass influences biodiversity including rodents. Given their roles in the ecosystem and responsiveness to habitat alterations, rodents are often used as model organisms for evaluating impacts of habitat modification on biodiversity [14–16]. At the same time, rodents can increase habitat heterogeneity and overall biodiversity by altering plant community composition and structure through soil disturbance, nutrient input, and foraging [17]. Therefore, habitat structure can influence rodent community structure, and rodent community structure can influence habitat structure [14–17]. Further, by consuming both plants and animals and being prey for higher order consumers, rodents are a critical energy link between producers and higher trophic level consumers in terrestrial food webs [18,19].

Habitat alterations that occur in managed forests, including both spatial (e.g., variation in management regimes across landscapes) and temporal (e.g., seasonal and successional changes), can influence wildlife community structure. Bowman et al. [20] determined that within stand vegetation structure explains the majority of differences in small mammal communities compared to landscape level variables. Variation in small
mammal population sizes is attributed mainly to difference in vegetation characteristics, but spatial variation of local processes for small mammals, such as dispersal, competition, and predation, can also influence community structure [20,21]. Rodent community structure (e.g., richness and diversity) is influenced by spatial changes in plant abundance and diversity through management options, such as retention of coarse woody debris, corridors, and streamside management zones [14,22–25]. Within forests, structural diversity provided by snags, downed logs and stumps (coarse woody debris), as well as understory and canopy development and composition, is particularly important for small mammals [15,24,26,27]. Different habitat elements provide options for thermoregulation, protection from predators, travel routes, and foraging and nesting habitat for various species [15,24,26,27].

Rodent communities also respond to temporal changes in forest structure, such as those associated with forest succession in managed pine stands or seasonal changes in vegetation [28,29]. For example, the rodent community might be dominated by omnivores (e.g., *Peromyscus leucopus*) in one-year-old pine plantations that consist primarily of annual plants, but herbivore rodent (e.g., *Sigmodon hispidus*) presence might increase in response to perennial grass appearance by the third year post-planting [28]. When canopy closure occurs in pine plantations in the seventh year, total rodent abundance decreases despite the increased occurrence of woodland species (e.g., *Neotoma floridana*) [28]. Managed forests with stands of different management regimes and successional stages provide habitat for various types of rodent communities.
Intercropping switchgrass in managed pine plantations converts a portion of the woody and herbaceous understory to one dominated by grass, which may alter rodent biodiversity [13,30]. In 2009, Marshall et al. [31] initiated a study in North Carolina to examine rodent community and population responses to switchgrass intercropping in a managed loblolly pine (Pinus taeda) plantation in the first two years after planting both pines and switchgrass. There was a shift in dominant species from the white-footed mouse (P. leucopus) to the hispid cotton rat (S. hispidus) between years 1 and 2 after treatment installation and when switchgrass became fully established [31]. However, in addition to changes associated with natural succession, there was a positive effect of switchgrass treatments on invasive, non-native house mouse (Mus musculus) abundance and a negative effect on abundance of native P. leucopus [31]. In the first year of the study, a significant increase in non-native house mouse (M. musculus) abundance coincided with the harvest of adjacent agriculture fields, suggesting these agriculture fields were the source for the immigration event [31].

Croplands support abundant populations of M. musculus due to few or no competitors and a large food supply, and individual mice migrate as resources change [32–34]. Mus musculus are omnivorous, and predate on invertebrates, seeds, and bird eggs, which can cause both direct and indirect changes in species distributions and densities [35–38]. The association of established switchgrass and M. musculus raises questions about the sustainability of biodiversity in a switchgrass intercropping management system [31]. However, the high abundance of M. musculus in switchgrass treatment plots from Marshall et al. [31] may be an artifact of 1) the site’s position within
a mixed forest/agriculture landscape where adjacent agriculture fields provided likely source populations of *M. musculus* and/or 2) the small scale of the study site, which allowed rodents to travel among treatment plots [18,31].

The objective of my study was to determine whether intercropping switchgrass in intensively managed loblolly pine plantations affected rodent community structure and population demographics when investigated at a large, landscape scale. I also examined whether abundance of *M. musculus* was influenced by switchgrass when surveyed at a scale relevant to both wildlife and forest managers and in the absence of a potential local agricultural source population. I hypothesized that the changes in forest understory vegetation associated with intercropping switchgrass in intensively managed pine plantations would influence rodent population demographics and community structure. When switchgrass is intercropped in pine forests, the vegetation between pine rows is replaced with one type of plant, switchgrass, which reduces habitat complexity. *Sigmodon hispidus* is a common grass-associated species in southeastern pine forests, therefore, I predicted that *S. hispidus* population abundance would increase with the presence of a grass-dominated understory in the intercropped stands [39]. As I predicted the increased abundance of only one rodent species and no effect on other species present, I also predicted a decrease in evenness and diversity in switchgrass intercropped treatments. I also predicted that *M. musculus* populations would not be influenced by the presence of switchgrass due to a lack of an agricultural source of *M. musculus*, because my research stands were isolated within a landscape-matrix dominated by intensively managed pine forest.
CHAPTER II
METHODS

Study Area and Experimental Design

To assess the sustainability of a switchgrass intercropping management system, Catchlight Energy LLC established the Kemper County, MS study site (32°52’N, 88°33’W) on land owned and maintained by Weyerhaeuser Company. Research stands were surrounded by a 25,000-ha landscape composed mostly (70%) of intensively managed pine (Pinus spp.) stands in different successional stages, mature pine-hardwood (17%), hardwood (10%), and non-forested areas (3%) [40]. The study area was intersected by unpaved access roads or fire lanes running along the forest edges, streamside management zones, and other set asides where appropriate (Figure 1).

Intensively managed loblolly pine (Pinus taeda) stands planted in 2005 were used as control stands. For the intercropped stands, Alamo switchgrass (Panicum virgatum L.) was planted in 2009 with a seed drill in alleys between pine beds in existing intensively managed pine stands that were also planted in 2005. Standard mechanical site preparation by Weyerhaeuser includes V-shearing of stumps and roots and sub-soiling to establish pine beds. Loblolly pine saplings were planted approximately 1.5 meters apart on raised beds that are spaced 6.1 meters apart, at a density of 450 trees/acre [40]. Harvest residuals (i.e. tops, limbs, and unmerchantable hardwoods) from the preceding clearcut harvest were left on site. For site preparation in intercropped stands, more extensive woody
debris and stump removal by additional V-blade passes were used to facilitate planting and germination of switchgrass. Fertilizer and herbicide were applied as needed. Pine trees in both intercropped and pine control stands typically are harvested at 27-35 years old, and switchgrass in the intercropped stands has been mowed and baled annually. Area of both intercropped and control stands ranged from 20.4 ha to 77.4 ha (mean = 41.0 ha, SE = 6.95 ha) (Figure 1). Distance between stands ranged from 1.3 km to 9.9 km (mean = 5.2 km, SE = 0.52 km) (Figure 1).

**Rodent Live-Trapping**

I live-trapped rodents July-October in 2011 and June-August in 2012. The first year of the study was considered preliminary to assess which rodent species were present. I live-trapped rodents using standard capture-mark-recapture methods as follows. Trapping grids consisted of 49 traps arranged 20 m apart in parallel lines to form a 7 ×7 grid. I placed the 14,400 m² (120 m × 120 m) trapping grid in an accessible location and > 20 m from the stand edge to avoid edge effects [41]. Each trap line contained six folding and/or non-folding 23-centimeter Sherman traps (H.B. Sherman Traps Inc., 167 Tallahassee, Florida, USA) and one randomly placed non-folding 18-centimeter Sherman trap or Longworth trap (Rogers Manufacturing Co., Peachland, British Columbia, Canada). I used small Sherman traps or Longworth traps to avoid trap bias towards larger rodents [42]. I obtained a collection permit from Mississippi Department of Wildlife, Fisheries, and Parks (# 0503127). I followed the American Society of Mammalogists guidelines for use of wild mammals [43] and was authorized by UNCG IACUC 11-03.
I baited each trap with rolled oats or a higher protein mixture of rolled oats and sunflower seeds on nights where the minimum temperature was \( \leq 40^\circ F \). I applied insecticide granules of pyrethrum (Talstar PL) around traps in areas with high fire ant activity. Use of pyrethroid insecticides for small mammal trapping deters imported fire ant activity without affecting capture and recapture success at that trap site [44,45]. I opened traps between 1700 and 2000 and then checked the following morning between 0500 and 1100. One period of trapping was three consecutive (when possible) nights of trapping. When first captured, I marked each rodent with a uniquely numbered ear-tag (Monel Numeric size 1005-1; National Band and Tag Co, Newport, Kentucky, USA). I recorded date, trap location, tag number, species, sex, age-class, mass, and reproductive state for each individual captured. I grouped white-footed mice (\( P. \) leucopus) and cotton mice (\( P. \) gossypinus) as Peromyscus spp. due to similarities in field identification characteristics and hybridization among these species [46,47]. I determined age class using a combination of body mass, fur characteristics, and reproductive state [48]. Individual \( S. \) hispidus were considered adults if they weighed > 80g [49]. I released captured shrews without being measured or marked.

Data Analyses

I measured rodent community using individual-based rarefaction curves, Smith and Wilson Evenness A Index (\( E_{wa} \)), and Simpson’s Diversity Index [50,51]. An individual-based rarefaction was used to compute the number of individuals for each sampling level to compare species richness between control and intercropped stands [52]. Community diversity can be split into two components: species richness (the number of
species captured in a grid) and species evenness [50,51]. $E_{var}$ was used, because it is an evenness index where richness is independent of evenness [50,51]. The Simpson’s Diversity Index measures dominance by identifying the likelihood that two chosen individuals will be the same species [50].

I examined $S. hispidus$ population demographics by estimating population abundance, recruitment, and survival, because this was the only rodent species I had sufficient data for using Program MARK [53]. Population abundance during each trapping period and survival probability (deaths and emigration) of adults between trapping periods was estimated using Pollock’s robust design models, with Huggins closed capture estimator [31]. Recruitment (births and immigration) was calculated using a robust design Pradel survival and recruitment model, with Huggins closed captures estimator [31,54]. Huggins closed capture estimator is a robust estimator for small sample sizes [31,55]. Robust models use > 1 capture occasion between survival intervals to produce estimates. I chose the best fit model parameters based on AICc values [53]. Abundance and survival model parameters included encounter probability, initial capture and recapture ($p$ and $c$), with time effects, group effects, time*group effects, and/or null effects and the probability of emigration from and staying away from the study site ($\gamma''$ and $\gamma'$). Recruitment model parameters included apparent survival ($f$) and recruitment ($\Phi$) probability with time and/or null effects, and I chose the appropriate parameters for encounter probabilities ($p$ and $c$) based on the parameters for the best fit model in the adult abundance models [53].
I used nonmetric multidimensional scaling (NMDS), with 50 random starts, to analyze similarity of rodent assemblages between treatments [56]. A scree plot was used to identify the appropriate number of dimensions, and final stress was used to show goodness-of-fit, with large values (> 0.20) indicating difficulty showing relationships among sites in the appropriate dimensions [56–60]. Bray-Curtis dissimilarity matrices were used to accommodate the large amount of zeros present in the dataset [61]. I used a two-way analysis of similarity (ANOSIM) to identify significant differences between treatments. Lastly, a similarity percentage (SIMPER) procedure identified the level each rodent species contributed to dissimilarity between treatments.

I calculated dependent variables for each trapping grid (~ 14,400 m²) over the entire season or for each trapping period, depending on the analysis procedure. I presented all data as untransformed (mean ± 1 standard error). Because I predicted a direction of effects, I report one-sided P-values. I determined whether my data were normally distributed using Shapiro-Wilk’s test, and homogeneity of variances was determined using Levene’s test. Where my data violated parametric assumptions, I either log or rank transformed the data. Dependent variables for my community level analysis included Simpson’s Diversity Index and Smith and Wilson Evenness A Index. I used separate Two Sample t-tests, with log transformed data when necessary, to compare each dependant variable between intercropped and pine control stands. Dependent variables for my population level analysis included population abundance, recruitment, and survival. For population level analyses that included abundance and survival, I calculated one value for each trapping period, and a repeated measures analysis of variance
(ANOVA) with rank transformed data was used to compare abundance and survival estimates between intercropped and control stands [62]. The independent variable in each test was the treatment type, and trapping period was included as the repeated measure. For recruitment, one value was calculated for the season. Therefore, I used a Two Sample $t$-test to compare recruitment between control and intercropped stands.

The repeated measure ANOVA was conducted in SAS 9.3 [63]. Two Sample $t$-tests, rarefaction analyses, and NMDS analyses were conducted using R 3.0.1 for Windows [64]. NMDS analyses were verified using Paleontological Statistics Software Package for Education and Data Analysis (PAST) software [65,66].
CHAPTER III

RESULTS

In 2011, I trapped 179 individuals (501 initial captures and recaptures) on 3 intercropped stands from July to October across 3,087 trap nights. Total unique individuals included 168 *Sigmodon hispidus*, 8 *Peromyscus* spp., 1 *Neotoma floridana*, 1 *Ochrotomys nuttalli* and 1 *Reithrodontomys humulis*. Incidental captures (initial capture and recaptures) included 31 *Cryptotis parva*. Trapping results in 2011 were used as preliminary data to assess which rodent species were present on intercropped stands. No formal analyses or comparisons were made.

In 2012, I trapped 374 unique individuals (902 initial captures and recaptures) on 8 stands (n = 4 intercropped and n = 4 control) from June to August across 8,232 trap nights. Total unique individuals included 331 *Sigmodon hispidus*, 32 *Peromyscus* spp., 7 *Oryzomys palustris*, 3 *Reithrodontomys humulis*, and 1 *Microtus pinetorum*. Incidental captures (initial capture and recaptures) included 197 *Cryptotis parva*, 1 *Sylvilagus floridanus*, and 1 *Tamias striatus*. One control stand received different site preparation and one intercropped stand suffered intense raccoon disturbance and, therefore, these two stands were removed from all analyses. Excluding these two stands resulted in 333 unique individuals (836 initial captures and recaptures) on 6 stands (n = 3 intercropped and n = 3 control) trapped across 6,174 trap nights. Total unique individuals on control stands included 73 *Sigmodon hispidus*, 21 *Peromyscus* spp., 3 *Oryzomys palustris*, and 2
Reithrodontomys humulis. Total unique individuals on intercropped stands included 227 Sigmodon hispidus, 4 Peromyscus spp., and 3 Oryzomys palustris. Sigmodon hispidus made up 90% of all captured individuals while Peromyscus spp. made up 7.5% of all captured individuals. Capture numbers of O. palustris, Peromyscus spp., and R. humulis were too low to be analyzed using Program MARK.

For community metrics, Simpson’s Diversity Index ($W = 0.89$, $P = 0.32$) was normally distributed whereas Smith and Wilson Evenness A Index was not normally distributed ($W = 0.67$, $P = 0.003$). Equal variances between groups were found for Smith and Wilson Evenness A Index ($t = 1.16$, $P = 0.34$) and Simpson’s Diversity Index ($t = 1.12$, $P = 0.35$). Therefore, Smith and Wilson Evenness A Index was log-transformed giving it a normal distribution ($W = 0.94$, $P = 0.64$) with equal variance ($t = 0.39$, $P = 0.57$). Parametric tests were used for both community metric comparisons. Smith and Wilson Evenness A Index ($t = 2.79$, $df = 4$, $P = 0.02$) and Simpson’s Diversity Index ($t = 2.64$, $df = 4$, $P = 0.03$) were significantly lower in intercropped stands (Table 1).

Rarefaction indicated lower species richness in intercropped stands (Figure 2). Using rarefaction curves, mean species richness between treatments was comparable at 103 sampled individuals with 4 species on control stands and 2.73 species on intercropped stands (Figure 2). Both intercropped and control rarefaction curves appeared to have leveled off during sampling (Figure 2).

For analyzing rodent assemblage similarity between treatments, a two-dimensional solution for the NMDS was determined to be appropriate based on the scree
plot and a minimum stress of 0.025. The NMDS plot showed possible clustering of the 3 control stands on one axis and the 3 intercropped stands on the second axis (Figure 3). Analysis of similarity (ANOSIM) showed no difference between treatments ($R = 0.81, P = 0.10$). Overall dissimilarity ($0 = \text{same and } 100 = \text{maximum distance observed}$) between control and intercropped stands was 53.74 with $S. \text{hispidus}$ contributing to over 86% of dissimilarity (Table 2).

*Sigmodon hispidus* was the only species with enough captures to calculate abundance, survival, and recruitment estimates in Program MARK. Based on AICc values from Program MARK, \{No Emigration M(t)\} contained the best fit model parameters for estimating $S. \text{hispidus}$ abundance and survival. For \{No Emigration M(t)\}, no movement of individuals was occurring between ‘observable’ and ‘unobservable’ states and initial capture and recapture probabilities changed with time (Table 3). For estimating $S. \text{hispidus}$ recruitment, \{p(t), ph(.), f(.)\} contained the best fit model parameters where initial capture and recapture probabilities for both stand types changed with time and apparent survival and recruitment did not change over time (Table 4).

*Sigmodon hispidus* abundance ($W = 0.90, P = 0.002$) and survival ($W = 0.54, P < 0.0001$) were not normally distributed whereas recruitment ($W = 0.87, P = 0.24$) showed a normal distribution. Equal variance between groups was found for $S. \text{hispidus}$ survival ($t = 1.88, P = 0.18$) and recruitment ($t = 0.03, P = 0.87$) whereas $S. \text{hispidus}$ abundance ($t = 5.86, P = 0.02$) showed unequal variances. Therefore, abundance and survival were rank-transformed for all population metrics comparisons. Population abundance of $S.$
hispidus was influenced by treatment ($F_{1,4} = 16.20, P = 0.02$), period ($F_{6,24} = 15.53, P < 0.0001$), and the treatment x period interaction ($F_{6,24} = 5.59, P = 0.001$) (Figure 4). Population abundance of S. hispidus increased through the season. Finally, I did not detect an influence of treatment ($t = -0.07, df = 4, P = 0.53$) on S. hispidus population recruitment or an influence of treatment ($F_{1,4} = 0.41, P = 0.56$), period ($F_{5,20} = 0.90, P = 0.50$), or treatment x period interaction ($F_{5,20} = 0.56, P = 0.73$) on survival (Table 5).
This study adds to the small body of literature on the impacts of intercropping switchgrass in managed pine forests on rodent populations and communities [31]. My findings indicate that intercropping switchgrass in managed pine plantations may have altered rodent community diversity and evenness by increasing abundance of *S. hispidus* but not other species. Marshall et al. [31] reported a positive association of invasive *M. musculus* with the presence of switchgrass. To the contrary, I did not capture *M. musculus* despite > 6,000 trap nights in an interior pine matrix. In another forest system, Robinson [67] compared small mammal community responses between row crop (i.e. soybeans, *Glycine max*) and an agroforest systems (i.e. cottonwood, *Populus deltoids*, and switchgrass) and found the agroforest systems maintained more complex vegetation structure through the year, which in turn supported a more abundant and diverse small mammal community. Although my study compared intensively managed forests with intercropped treatments, I also found that rodent community diversity changed with a switchgrass intercropping system. I found a decrease in rodent community diversity that was attributed to the decrease in evenness caused by increased *S. hispidus* abundance.

My results supported my hypothesis that intercropping switchgrass in intensively managed pine plantations would influence rodent population demographics and community structure because of changes to forest understory vegetation [31,67]. Many
studies have demonstrated that rodent communities respond to changes in forest structure from different forest management regimes [14,22,23,31,67–70]. For example, in pine plantations 1-5 years post-establishment, total rodent abundance, excluding *Peromyscus* spp., responded to the changes in vegetation caused by the different intensities of site preparation [68]. Low-intensity site establishment practices (mechanical- or chemical-only site preparation) contained denser vegetation than the high establishment intensity (mechanical and chemical site preparation with broadcast herbaceous control) and had greater abundances of *N. floridana, R. fulvescens,* and *S. hispidus* [68].

My results suggest that the higher *S. hispidus* abundance in intercropped stands contributed to the majority of dissimilarity between treatments causing rodent community evenness to decrease in intercropped stands, which decreased community diversity. Intercropping switchgrass in managed pine forest changes the dominant understory structure from woody/herbaceous vegetation to grass vegetation [30], thus promoting the presence of *S. hispidus,* an herbivore that prefers grass [26]. Similarly, *S. hispidus* was the most abundant species in intercropped treatments by two years after switchgrass establishment in North Carolina [31]. The difference in *S. hispidus* abundance and community structure between control and intercropped treatments suggests that the rodent community responded to the alterations to the understory vegetation and that intercropped stands provide resources that are capable of maintaining herbivore (e.g., *S. hispidus*) populations with higher abundances.
Although *S. hispidus* population abundance was significantly higher in intercropped stands than control stands, *S. hispidus* was still the dominant rodent species in both intercropped and control stands. Even though *Peromyscus* spp. was found in low numbers, it was the second most common rodent captured in both stand types. I could not distinguish *P. leucopus* and *P. gossypinus* during my study, but both species are omnivorous and considered microhabitat generalists [24,26,46,47,71,72]. *Sigmodon hispidus* is often a dominant rodent species in young to intermediate age pine plantations in southeastern United States [28,73]. In 2- to 4-year-old Georgia pine plantations, *S. hispidus* was the dominant rodent, while *P. leucopus* was the second most common species found [28]. Hanberry et al. [68] investigated pine plantation establishment treatments in Mississippi ranging from low to high intensity during years 1-5 post-establishment and reported that *Peromyscus* spp. and *S. hispidus* were the most dominant rodent species across treatments and years. Even though rodent community diversity in my study decreased in intercropped stands, *S. hispidus* and *Peromyscus* spp. still accounted for 90% and 7.5% of captures in both stand types.

My rodent community results suggest that by planting and maintaining a dense, grass-dominated understory in intercropped stands, the period of early succession may be extended so that early successional rodent species continue to be major components of the community [26,28]. After a mature pine stand is harvested, herbaceous vegetation will colonize the newly disturbed site [14]. Increases in soft mast and insects from growth of early successional vegetation following clearcuts result in a higher abundance of rodents [70]. As the loblolly pine canopy closes around year 6, dense thickets of woody
vegetation, such as blackberry (*Rubus* spp.), develop around the rows of pine [73]. Canopy closure results in reductions of understory and rodent abundance [70,74]. Increasing grass vegetation through intercropping may benefit herbivorous rodents (e.g., *S. hispidus*) that use early successional vegetation for cover, nesting, and food resources [14].

In addition to *S. hispidus* population abundance being higher in switchgrass intercropped stands, I also observed an increase in *S. hispidus* abundance through trapping periods and as switchgrass grew. Other rodent species had low abundances that possibly prevented detection of temporal changes in populations. Switchgrass is a warm-season perennial that is harvested annually, in the fall or winter after senescence, as a biofuel feedstock at the Kemper County study site. Therefore, it is only available to wildlife during a portion of the year [13]. The number of small mammal captures decreases after mowing occurs, but pine tree beds in intercropped stands could provide refugia to rodents after switchgrass harvesting [75,76]. *Sigmodon hispidus* abundance is known to fluctuate during the year due to seasonal weather conditions and resource availability [29]. Winter conditions will cause *S. hispidus* abundance to be lower the following spring, but abundance will increase into the fall as weather conditions improve and habitat vegetation changes [29].

All rodent species captured during my study were known to be at the Kemper County study site from a previous study [16], but few *Neotoma floridana, Ochrotomys nuttalli, Oryzomys palustris, Reithrodontomys humulis,* and *Microtus pinetorum*
individuals were captured due to their known preference for different habitat types than I studied [16,26,68,71,77–81]. *Neotoma floridana* prefers older forested habitat with relatively open understory and closed overstory canopy [81]. *Ochrotomys nuttalli* are similar in body size and share similar food resources and nest site preferences with *Peromyscus* spp., but difference in 3-dimensional habitat use (i.e. vertical vegetation use by *O. nuttalli*) provides enough niche segregation to coexist [26,78,79]. *Oryzomys palustris* are wetland rodent species that sometimes use upland habitats depending on population demography, environmental conditions and prey availability [80]. *Reithrodontomys humulis* are found on southeastern pine plantations in very early successional stages, so it was unlikely that they would be present on 6-7 year-old pine stands [16,26,68,71]. *Microtus pinetorum* is a habitat generalist found mostly in mid- to late-successional forests, and low number of captures is likely due to its semi-fossorial nature [71]. It is possible *M. pinetorum* was present in higher numbers on the study stands, but my trapping method may not have been optimal for catching voles [77].

My results suggest that *M. musculus* is not associated with switchgrass when agricultural crop resources to sustain the population are not adjacent to the switchgrass treatments [31–34]. *Mus musculus* was not captured on any of my study stands but are known to be present in the area based on trapping efforts during previous years and even during 2012 on other forest stands [16]. *Mus musculus* is an invasive, non-native rodent that is known to have high abundances when an abundant resource, such as an agriculture crop, is available [31–34]. In the absence of an abundant food resource, such as in forest habitats, *M. musculus* maintain lower population abundances [16,28,33]. Therefore, my
results suggest that intercropping switchgrass in pine plantations does not promote the presence of *M. musculus*.

The results of my study demonstrate the importance of investigating wildlife populations and communities, namely rodents, at a landscape scale. Marshall et al. [31] investigated the effects of a switchgrass intercropping system at a small-scale study site adjacent to agriculture land, which influenced the rodent community by providing a source population of *M. musculus*. Results from Marshall et al. [31] suggested that intercropping switchgrass in pine plantations promotes the presence *M. musculus*, which raises questions about the sustainability of a switchgrass intercropping system [31]. However, my results show that when a switchgrass intercropping system is investigated following establishment and at a landscape scale where the treatment stands are isolated in a forest matrix, switchgrass does not promote the presence of *M. musculus*. Different landscape variables (e.g., agriculture) can influence the types of rodent communities present found in an area [21,82].

*Management Implication and Future Direction*

My results suggest that a switchgrass intercropping management system increases the biomass of a native rodent, *S. hispidus*, which is commonly the most abundant rodent in southeastern pine forests. The rest of the rodent community appears to be unaffected. Other demographics (i.e. survival and recruitment) did not differ between control and intercropped stands. Therefore, my results support the idea that a switchgrass
intercropping system to produce biofuel feedstock might be a sustainable option for planting switchgrass.

My study contributes to a growing body of research demonstrating the sustainability of an intercropping system through investigating impacts on biodiversity and productivity. In a two-year study, Homyack et al. [83] showed that intercropping switchgrass in pine plantations does not affect herptefauna abundance and diversity. At the same site, Briones et al. [84] showed that \textit{P. leucopus} maintained its trophic position in both switchgrass intercropping systems and pine stands, indicating that food web interactions and ecosystem services linked to \textit{P. leucopus} are not affected by switchgrass intercropping. Iglay et al. [85] showed that switchgrass intercropped in pine stands \( \geq 5 \) years old initially promotes a more diverse herbaceous plant community. Loman et al. [40] found that site preparation for intercropped and traditional pine plantations produced similar dispersal and volume of coarse woody debris (CWD), which provides important habitat for many mammals and herptefauna. In a study designed to examine productivity, Albaugh et al. [86] found that intercropping pine and switchgrass does not affect leaf-level gas exchange (i.e. photosynthesis or stomatal conductance) or water potential for neither pine nor switchgrass. At this time, intercropping switchgrass in pine plantations can be considered sustainable, because no negative impacts on ecosystem biodiversity and functioning have been observed [40,83–86].

My conclusion is based on observations made in 2012 by surveying pine stands planted in 2005 and switchgrass intercropped in 2009. Effects of switchgrass
intercropping at early stages of establishment on rodent communities cannot be
determined without further investigation. Measuring microhabitat changes associated
with intercropping switchgrass and examining individual rodent responses to these
changes could be used to determine ecological mechanisms influencing rodent
communities, which is important for determining long-term management implications.
REFERENCES


[58] J.B. Kruskal, Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis, Psychometrika, 29 (1964) 1–27.


[66] Paleontological Statistics Software Package for Education and Data Analysis (PAST) software, R Development Core Team, 2010.


Table 1. Untransformed mean (± 1SE) values for Smith and Wilson Evenness A Index and Simpson’s Diversity Index from live-trapping pine control stands (n = 3) and intercropped stands (n = 3) in Kemper County, Mississippi. We examined treatment differences of evenness and diversity with a Two Sample $t$-test. P-values are reported as one-sided.

<table>
<thead>
<tr>
<th></th>
<th>Smith and Wilson Evenness A</th>
<th>Simpson's Diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Control</strong></td>
<td>0.41 ± 0.24</td>
<td>0.40 ± 0.12</td>
</tr>
<tr>
<td><strong>Intercropped</strong></td>
<td>0.05 ± 0.02</td>
<td>0.05 ± 0.05</td>
</tr>
</tbody>
</table>

$t = 2.79$, df = 4, $P = 0.02$  $t = 2.64$, df = 4, $P = 0.03$
Table 2. SIMPER results from nonmetric multidimensional scaling of pine control stands (n = 3) versus intercropped stands (n = 3). Contribution is based on the overall dissimilarity of 53.74, cumulative percent is the percentage each species contributed to the overall dissimilarity, and the mean abundances of each species per specified treatment are provided for comparison.

<table>
<thead>
<tr>
<th>Species</th>
<th>Contribution %</th>
<th>Cumulative %</th>
<th>Mean abundance in Control</th>
<th>Mean abundance in Intercropped</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sigmodon hispidus</em></td>
<td>86.13</td>
<td>86.13</td>
<td>24.3</td>
<td>75.7</td>
</tr>
<tr>
<td><em>Peromyscus spp.</em></td>
<td>10.44</td>
<td>96.57</td>
<td>7</td>
<td>1.33</td>
</tr>
<tr>
<td><em>Oryzomys palustris</em></td>
<td>2.286</td>
<td>98.86</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>Reithrodontomys humulis</em></td>
<td>1.142</td>
<td>100</td>
<td>0.667</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 3. Program MARK output for Pollock’s robust design models with Huggins closed capture estimator used to select the best fit model parameters for estimating *Sigmodon hispidus* abundance and survival. Model parameters included encounter probability (M), initial capture and recapture, with time effects (t), group effects (b), time*group effects (tb), and/or null effects (.) and the probability of emigration from and staying away from the study site (No emigration, Random, or Markovian). Raw data was obtained from live-trapping pine control stands (n = 3) and intercropped stands (n = 3) in Kemper County, Mississippi.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>Delta AICc</th>
<th>AICc Weight</th>
<th>Model Likelihood</th>
<th>No. Par.</th>
</tr>
</thead>
<tbody>
<tr>
<td>{No Emigration M(t)}</td>
<td>2340.89</td>
<td>0</td>
<td>0.94591</td>
<td>1</td>
<td>40</td>
</tr>
<tr>
<td>{No Emigration M(.)}</td>
<td>2348.387</td>
<td>7.497</td>
<td>0.02228</td>
<td>0.0236</td>
<td>34</td>
</tr>
<tr>
<td>{No Emigration M(tb)}</td>
<td>2348.574</td>
<td>7.6839</td>
<td>0.02029</td>
<td>0.0215</td>
<td>46</td>
</tr>
<tr>
<td>{No Emigration M(b)}</td>
<td>2349.707</td>
<td>8.8167</td>
<td>0.01152</td>
<td>0.0122</td>
<td>35</td>
</tr>
<tr>
<td>{Random M(t)}</td>
<td>2374.927</td>
<td>34.0369</td>
<td>0</td>
<td>0</td>
<td>67</td>
</tr>
<tr>
<td>{Random M(b)}</td>
<td>2377.456</td>
<td>36.5656</td>
<td>0</td>
<td>0</td>
<td>62</td>
</tr>
<tr>
<td>{Random M(.)}</td>
<td>2378.057</td>
<td>37.1664</td>
<td>0</td>
<td>0</td>
<td>61</td>
</tr>
<tr>
<td>{Markovian M(b)}</td>
<td>2395.735</td>
<td>54.8443</td>
<td>0</td>
<td>0</td>
<td>75</td>
</tr>
<tr>
<td>{Markovian M(t)}</td>
<td>2395.984</td>
<td>55.0941</td>
<td>0</td>
<td>0</td>
<td>80</td>
</tr>
<tr>
<td>{Markovian M(.)}</td>
<td>2397.329</td>
<td>56.4388</td>
<td>0</td>
<td>0</td>
<td>74</td>
</tr>
<tr>
<td>{Markovian M(tb)}</td>
<td>2400.751</td>
<td>59.8604</td>
<td>0</td>
<td>0</td>
<td>86</td>
</tr>
<tr>
<td>{Random M(tb)}</td>
<td>2402.701</td>
<td>61.811</td>
<td>0</td>
<td>0</td>
<td>81</td>
</tr>
</tbody>
</table>
Table 4. Program MARK output for Pradel survival and recruitment model with Huggins closed captures estimator used to select the best fit model parameters for estimating *Sigmodon hispidus* recruitment. Model parameters included apparent survival (f) and recruitment (ph) probability with time (t) and/or null effects (.), and the appropriate parameters for encounter probabilities (p) were chosen based on the parameters for the best fit model in the adult abundance models. Raw data was obtained from live-trapping pine control stands (n = 3) and intercropped stands (n = 3) in Kemper County, Mississippi.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>Delta AICc</th>
<th>AICc Weight</th>
<th>Model Likelihood</th>
<th>No. Par.</th>
</tr>
</thead>
<tbody>
<tr>
<td>{p(t), ph(., f(.))}</td>
<td>4067.1042</td>
<td>0</td>
<td>0.99995</td>
<td>1</td>
<td>19</td>
</tr>
<tr>
<td>{p(t), ph(., f(t))}</td>
<td>4087.0418</td>
<td>19.9376</td>
<td>0.00005</td>
<td>0.0001</td>
<td>45</td>
</tr>
<tr>
<td>{p(t), ph(t), f(.)}</td>
<td>4091.6482</td>
<td>24.544</td>
<td>0</td>
<td>0</td>
<td>43</td>
</tr>
</tbody>
</table>
Table 5. Untransformed mean (± 1SE) recruitment estimates, new individual via birth or immigration/existing member/trapping grid, for *Sigmodon hispidus* by treatment calculated in Program MARK; statistical results are from comparisons using a Two Sample *t*-test calculated in R. Untransformed mean (± 1SE) survival estimates for *Sigmodon hispidus* for inter-trapping period intervals by treatment (averaged across time and trapping grids within treatment); calculated in Program MARK; statistical results are from comparisons using repeated measures ANOVA calculated in SAS. P-values are reported as one-sided. Raw data for recruitment and survival estimates were obtained from live-trapping pine control stands (n = 3) and intercropped stands (n = 3) in Kemper County, Mississippi.

<table>
<thead>
<tr>
<th></th>
<th>Recruitment</th>
<th>Survival</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Control</strong></td>
<td>0.11 ± 0.02</td>
<td>0.83 ± 0.08</td>
</tr>
<tr>
<td><strong>Intercropped</strong></td>
<td>0.11 ± 0.03</td>
<td>0.92 ± 0.02</td>
</tr>
</tbody>
</table>

\[ t = -0.07, \text{df} = 4, P = 0.53 \]

\[ F_{1,4} = 0.41, P = 0.56 \]
APPENDIX B

FIGURES

Figure 1. I examined rodent community structure and population demographics on intercropped stands (n = 3) and pine control stands (n = 3) in Kemper County, MS, USA. The study site was established by Catchlight Energy LLC on land owned by Weyerhaeuser Company. Live-trapping grids within each stand were 14,400 m². The study site is highlighted in red on the inset map.
Figure 2. Rarefaction curves showing the expected number of rodent species on intercropped and pine control stands for any given number of individuals. Raw data was obtained from live-trapping (6,174 trap nights) using 14,400 m$^2$ (120 m × 120 m) trapping grids in control (n = 3) and intercropped (n = 3) treatments in 2012.
Figure 3. Nonmetric multidimensional scaling (NMDS) plot of small mammal communities by treatment (n = 3) in Kemper County, MS, USA in 2012. NMDS plots show the relative relationships among sites. Stress = 0.025
Figure 4. Untransformed population abundance estimates (mean abundance ± 1 standard error) from Program MARK for *Sigmodon hispidus* by trapping period. Raw data was obtained from live-trapping (6,174 trap nights) using 14,400 m² (120 m × 120 m) trapping grids in control (n = 3) and intercropped (n = 3) treatments. Seven trapping periods took place from June to August 2012.