

## Response of rodent community structure and population demographics to intercropping switchgrass (*Panicum virgatum*) within loblolly pine (*Pinus taeda*) plantations in a forest-dominated landscape

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### Abstract:

Intercropping switchgrass (*Panicum virgatum*) in existing managed pine (*Pinus* spp.) forests potentially can produce a biofuel feedstock without encumbering additional arable land. However, it is not clear how intercropping, which changes understory vegetation composition and structure, may influence rodent communities. Therefore, as part of a broader effort to examine ecological sustainability of an intercropping management system, we investigated whether intercropping switchgrass in intensively managed loblolly pine (*Pinus taeda*) stands affected rodent community structure and population demographics in a managed forest landscape. We conducted seven live-trapping sessions during June–August 2012 on three intensively managed pine stands (control) and three intensively managed pine stands intercropped with switchgrass (treatment). Pine stands intercropped with switchgrass had lower rodent community evenness ( $P = 0.02$ ) and diversity ( $P = 0.03$ ) than control stands primarily because of greater hispid cotton rat (*Sigmodon hispidus*) abundance in intercropped stands ( $P = 0.02$ ). However, there was no treatment effect on cotton rat survival or recruitment. Our results suggest the switchgrass intercropping system in our study influenced rodent community structure via effects on hispid cotton rats during the early successional stage of a loblolly pine stand.

**Keywords:** *Panicum virgatum* | *Pinus taeda* | Rodent | Biofuel | Mississippi | Forest management

### Article:

#### 1. Introduction

Intercropping biofuel feedstocks in managed forests is a potential method to produce cellulosic energy sources and avoid or reduce land conversion risks [1], [2]. Switchgrass (*Panicum virgatum*) has long been considered a promising biofuel feedstock. 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 [3], [4], [5], [6], [7]. Further, perennial grasses such as switchgrass can provide habitat conditions favorable for native grassland birds, and likely other species associated with open-canopy, grassy habitat types [8], [9]. In addition, it may be feasible to intercrop switchgrass in intensively managed pine (*Pinus* spp.) stands, which avoids the “fuel versus food” debate that has hampered other feedstocks [3], [10], [11].

Past research has demonstrated that managed pine forests can contribute to local and regional biodiversity (e.g., [12], [13]). However, intercropping switchgrass in intensively managed pine stands converts a portion of the woody and herbaceous understory to a grass-dominated structure [14], which may influence biodiversity and thus ecological sustainability [10]. A growing body of research has investigated effects of intercropping switchgrass in intensively managed loblolly pine (*Pinus taeda*) stands on biodiversity. In North Carolina, U.S.A., intercropping pine and switchgrass in intensively managed pine stands did not affect herpetofauna abundance and diversity [15] the first two years after establishment nor did it influence trophic position of white-footed mice (*Peromyscus leucopus*) [16], indicating that food web interactions and ecosystem services linked to mice were not affected by switchgrass intercropping. In Mississippi, U.S.A., stand establishment for intercropping vs. “traditional” pine management reduced abundance of neotropical migrants and forest-edge associated bird species in the first two years after planting and caused an increase in abundance in the third year [17]. Further, in Mississippi, initial intercropping reduced snag abundance but maintained similar volumes of coarse woody debris (CWD; [18]), which provides important habitat structure for numerous species of rodents.

Although these studies provide some insight, it is still unclear how intercropping switchgrass affects wildlife communities, including rodents, in these forested systems. Given their numerous ecological roles and responsiveness to habitat alteration, rodents are often used as model organisms for evaluating effects of vegetation change on biodiversity [19], [20], [21]. By consuming both plants and animals and by being prey for higher order consumers, rodents are a critical energy link between producers and higher trophic level consumers in terrestrial food webs [22], [23]. Rodents also can increase habitat heterogeneity and overall biodiversity by altering plant community composition and structure through soil disturbance, nutrient input, foraging, and seed and spore dispersal [24]. Therefore, vegetation composition and structure can influence rodent community structure, and rodent community structure can affect habitat structure [19], [20], [21], [24].

Recent work has examined effects of intercropping switchgrass on rodent communities, but numerous questions remain. At a small-scale, (plot size ~ 1 ha), research site in North Carolina, U.S.A., within an agriculture/agroforestry landscape matrix, switchgrass was intercropped with loblolly pine to evaluate sustainability of intercropping switchgrass in intensively managed pine stands. At that experimental research site, rodent community richness and diversity did not differ between intercropped and traditional treatments 1–4 years post site preparation [25], [26]. However, during this time, the dominant species switched from white-footed mouse to hispid

cotton rat (*Sigmodon hispidus*) as the understory structure changed [25], [26]. Additionally, switchgrass negatively affected abundance of native white-footed mice and positively affected abundance of invasive, non-native house mice (*Mus musculus*) [25]. This result may have been potentially influenced by nearby agriculture fields as a source of house mice [25]. By year 4 post-treatment, house mice primarily were found in the monoculture switchgrass treatment [26]. The link between switchgrass establishment and house mouse occupancy raises further questions about sustainability of rodent communities in a switchgrass intercropping management system. However, it is unclear whether house mice respond similarly at a larger spatial scale in different landscape contexts.

To better understand how intercropping may influence rodent communities, we examined if intercropping switchgrass in intensively managed loblolly pine stands affected rodent community structure and population demographics in a managed pine landscape. In addition, we investigated whether abundance of house mice was influenced by intercropping switchgrass at a larger spatial scale (25,000 ha compared to the 33.4 ha research site previously examined in Homyack et al. [26]) and in a predominantly forested landscape. We hypothesized changes in vegetation communities associated with intercropping switchgrass in intensively managed pine stands would influence rodent population demographics and community structure. We predicted abundance of hispid cotton rats would increase because intercropping increases the grass component of vegetation within intensively managed pine stands [14] and because of known positive relationships between herbaceous cover and this species [27], [28], [29]. We thus predicted a decrease in evenness and diversity in switchgrass intercropped treatments. Contrary to previous studies that found the house mouse was associated with switchgrass, we predicted the house mouse would be absent from our forested landscape due to a lack of an agricultural source of house mice as compared to the small-scale research site in North Carolina, U.S.A.

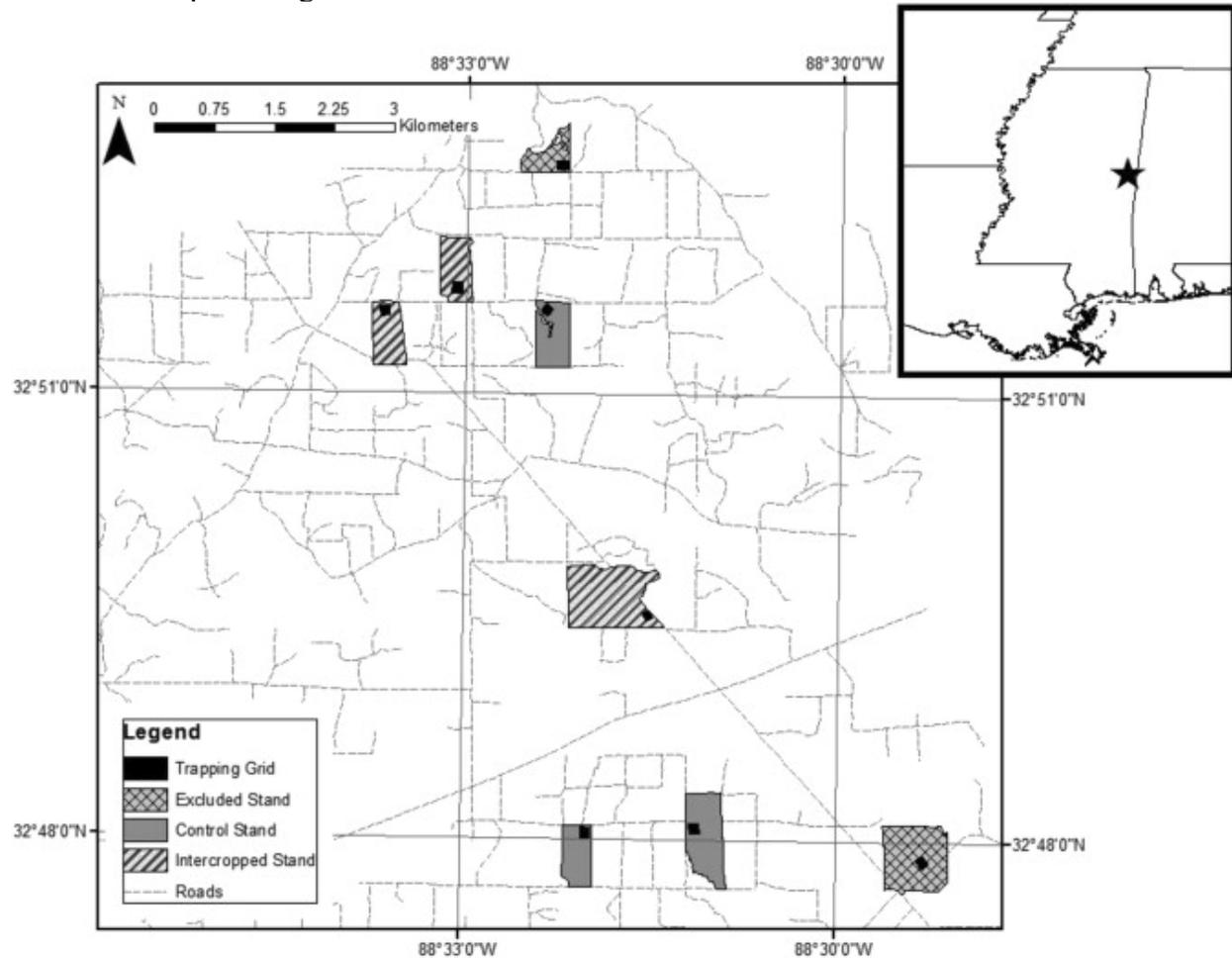
## **2. Materials and methods**

### **2.1. Study area and experimental design**

To assess biodiversity consequences of a switchgrass intercropping management system, Weyerhaeuser Company and Catchlight Energy LLC, a joint venture between Chevron and Weyerhaeuser Company, established a study area in east-central Mississippi (Kemper County), USA (32°52'N, 88°33'W) on land owned and managed by Weyerhaeuser Company. Research stands were embedded in a 25,000 ha landscape composed of intensively managed pine (*Pinus* spp.) stands in different successional stages (70%), mature pine-hardwood (17%), hardwood (10%), and non-forested areas (3%) [18]. The study area was intersected by unpaved access roads and fire lanes that separated forest stands, mature forest buffers along streams, and other unmanaged areas (Fig. 1).

We used intensively managed loblolly pine stands planted in winter 2005 as control stands. Control stands were mechanically site-prepared during summer 2004 and received a banded chemical weed control treatment during the first growing season (spring 2005). Standard mechanical site preparation included shearing of stumps and roots with a V-shaped blade attached to a bulldozer and sub-soiling to establish raised planting beds for pine seedlings. Loblolly pine seedlings (1 year old) were planted at a 1.5 × 6.1 m spacing, or an areal density of

1100 ha<sup>-1</sup>[18]. Tops, limbs, and unmerchantable hardwoods were left on site following clearcut harvest of the preceding stand.



**Fig. 1.** Kemper County, Mississippi, USA, study site. In 2012, we examined rodent community structure and population demographics on intercropped stands ( $n = 3$ ) and pine control stands ( $n = 3$ ) in Kemper County, Mississippi, U.S.A. The study site was established by Catchlight Energy LLC on land owned by Weyerhaeuser Company. Live-trapping grids within each stand were 14,400 m<sup>2</sup>. The study site is marked using a star symbol on the inset map.

Our treatment stands were established in winter 2005 using methods outlined above but had ‘Alamo’ accession of switchgrass (*P. virgatum*) planted in spring 2009 with a seed drill in 6.1 m alleys between pine rows. In these intercropped stands, more extensive woody debris and stump removal occurred in alleys between rows of pine trees, as compared to control stands, to facilitate seeding and germination of switchgrass. As expected, intercropped stands had increased grass coverage on and between pine beds when compared to control stands, which were composed of mostly perennial semi-woody vines and shrubs such as sawtooth blackberry (*Rubus argutus*) and American beautyberry (*Callicarpa americana*) [14].

Pine trees in this system typically are thinned at 11–15 years of age and then harvested 27–35 years after planting, and switchgrass was mowed and baled annually during fall and winter.

Control and treatment stands were 20.4–77.4 ha ( $41.0 \pm 6.95$  ha) in size and the distance between stands ranged from 1.3 to 9.9 km ( $5.2 \pm 0.52$  km) (Fig. 1).

## 2.2. Rodent live-trapping

We live-trapped rodents during June–August 2012 using standard capture-mark-recapture methods. In each stand, we established a 14,400 m<sup>2</sup> (120 m × 120 m) trapping grid consisting of 49 traps arranged 20 m apart in parallel lines to form a 7 × 7 grid. We established the trapping grid in an accessible location of each stand >20 m from an edge to avoid edge effects [30], [31] and to facilitate trapping logistics to minimize travel time into forest stands. Edge effects were not expected due to the small home ranges of rodents [31]. We did not observe any obvious edge effects translated in variation in capture data. For each trapping grid, we established the first trap in the corner on a pine bed. Each trap line ran parallel to the pine beds. Starting at the first line, which was a pine bed, each trap line was placed 20 m apart. Therefore, the percentage of switchgrass (~70% on treatment plots) and pine cover (~30%) on each trapping grid was similar. Each trap line contained six folding and/or non-folding 23-cm Sherman traps (H.B. Sherman Traps Inc., Tallahassee, Florida, U.S.A.) and one randomly placed non-folding 18-cm Sherman trap or Longworth trap (Rogers Manufacturing Co., Peachland, British Columbia, Canada) to trap small, juvenile individuals and avoid trap bias towards larger rodents [16], [25], [26], [32]. We followed the American Society of Mammalogists guidelines for use of wild mammals [33] and our field methods were approved by UNCG IACUC 11-03 with permission from the Mississippi Department of Wildlife, Fisheries, and Parks (# 0503127).

We baited each trap with rolled oats or rolled oats and sunflower seeds on nights when the minimum temperature was  $\leq 4$  °C (2 nights). We applied insecticide granules of pyrethrum (Talstar PL) around traps in areas with high fire ant (*Solenopsis* spp.) activity to prevent these non-native species from harming captured rodents without affecting capture or recapture success at that trap site [34], [35]. We opened traps after 1700 and checked them the following morning beginning at approximately 0500. In each trapping period, we trapped all stands for three consecutive nights. Occasionally, the three consecutive nights were interrupted by sudden, severe weather events. However, trapping resumed the following day. We trapped for 7 periods in this study. Therefore, trapping effort was the same for both control and intercropped treatments. We marked each rodent with a uniquely numbered ear-tag (Monel Numeric size 1005-1; National Band and Tag Co, Newport, Kentucky, USA) upon initial capture. We recorded date, trap location, tag number, species, sex, age-class (juvenile or adult), mass (g), and reproductive state (reproductive or not reproductive) for each individual captured. We grouped white-footed mice (*P. leucopus*) and cotton mice (*Peromyscus gossypinus*) as *Peromyscus* spp. due to similarities in field identification characteristics and known hybridization between these species [36], [37]. We determined age class using a combination of body mass, pelage characteristics, and reproductive state [38]. Individual cotton rats were considered adults if they weighed >80 g [39]. We released all shrews (Soricidae) without measurement or marking.

## 2.3. Statistical analyses

We examined treatment responses by the rodent community with the Smith and Wilson Evenness A Index ( $E_{\text{var}}$ ) and Simpson's Diversity Index (D) [40], [41]. We selected Smith and

Wilson Evenness A Index because it is independent of richness [40], [41]. The Simpson's Diversity Index measures dominance by identifying likelihood that two chosen individuals will be the same species and thus incorporates both richness and abundance [40]. We used non-metric multidimensional scaling (NMDS) with 50 random starts to analyze similarity of rodent assemblages [42]. We used a scree plot to identify the appropriate number of dimensions and final stress to evaluate goodness-of-fit, with large values ( $>0.20$ ) indicating difficulty showing relationships among sites in the appropriate dimensions [42], [43], [44], [45], [46]. We used Bray–Curtis dissimilarity matrices to accommodate the large number of zero captures in our dataset [47]. We used a one-way analysis of similarity (ANOSIM) to identify significant differences between treatments [43]. Lastly, we used a similarity percentage (SIMPER) procedure to identify the level each rodent species contributed to dissimilarity between treatments [43].

Dependent variables for our population-level analysis included population abundance, recruitment, and survival. We estimated population abundance, survival, and recruitment in Program MARK using recapture and age data from live-trapping. We estimated population abundance and survival probability (deaths and emigration) of adult mice using Pollock's robust design models, with Huggins closed capture estimator [48], [49]. Model parameters included encounter probability ( $M$ ), initial capture and recapture, with time (trapping period) effects ( $t$ ), group (stand) 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) [50]. We calculated recruitment (new individual via birth or immigration/existing member/stand) using a robust design Pradel survival and recruitment model, with Huggins closed captures estimator, which is robust for small sample sizes [25], [51]. For recruitment, juveniles were included if they were recaptured as adults. Model parameters included apparent survival ( $ph$ ) and recruitment ( $f$ ) 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 model [50].

We chose the best fit model parameters based on Akaike information criterion ( $AIC_C$ ) values [50]. For abundance and survival estimates, the best fit model selected included no emigration with time effects (Table 1). Because time effects were found for abundance and survival, an abundance value was calculated for each trapping period (7 trapping periods per stand) and a survival value was calculated for each interval between trapping periods (6 intervals per stand). For recruitment estimates, the best fit model included time effects for encounter probability and null effects for apparent survival and recruitment (Table 2). Because time effects were not included in the model for recruitment ( $AIC_C = 0$ ), one recruitment value was calculated for each stand (3 intercropped and 3 control).

Thus, we calculated dependent variables for each trapping grid with abundance and survival calculated for each trapping period on each grid, and recruitment, diversity, and evenness over the entire season. For population-level analyses that included abundance and survival, we used a repeated measures analysis of variance (ANOVA) with rank-transformed data to examine treatment effects across trapping periods (repeated measure) with treatment type as the independent variable [52]. For recruitment, we used a two sample  $t$ -test to compare estimated recruitment from Program MARK between control and intercropped stands. For community-

level analyses that included diversity and evenness, we used separate two sample  $t$ -tests, with log-transformed data when necessary, to compare  $E_{var}$  or  $D$  values between intercropped and pine control stands.

**Table 1.** 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 ( $\cdot$ ) 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.

Model	AIC <sub>c</sub>	Delta AIC <sub>c</sub>	AIC <sub>c</sub> weight	Model likelihood	No. par.
{No Emigration M( $t$ )}	2340.89	0	0.94591	1	40
{No Emigration M( $\cdot$ )}	2348.387	7.497	0.02228	0.0236	34
{No Emigration M( $tb$ )}	2348.574	7.6839	0.02029	0.0215	46
{No Emigration M( $b$ )}	2349.707	8.8167	0.01152	0.0122	35
{Random M( $t$ )}	2374.927	34.0369	0	0	67
{Random M( $b$ )}	2377.456	36.5656	0	0	62
{Random M( $\cdot$ )}	2378.057	37.1664	0	0	61
{Markovian M( $b$ )}	2395.735	54.8443	0	0	75
{Markovian M( $t$ )}	2395.984	55.0941	0	0	80
{Markovian M( $\cdot$ )}	2397.329	56.4388	0	0	74
{Markovian M( $tb$ )}	2400.751	59.8604	0	0	86
{Random M( $tb$ )}	2402.701	61.811	0	0	81

**Table 2.** 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 ( $\cdot$ ), 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.

Model	AIC <sub>c</sub>	Delta AIC <sub>c</sub>	AIC <sub>c</sub> weight	Model likelihood	No. par.
{ $p(t)$ , $ph(\cdot)$ , $f(\cdot)$ }	4067.1042	0	0.99995	1	19
{ $p(t)$ , $ph(\cdot)$ , $f(t)$ }	4087.0418	19.9376	0.00005	0.0001	45
{ $p(t)$ , $ph(t)$ , $f(\cdot)$ }	4091.6482	24.544	0	0	43

We determined whether our data were normally distributed using Shapiro–Wilks' test and homogeneity of variances with Levene's test. We log- or rank-transformed data when parametric assumptions were violated. Abundance and survival were rank-transformed for all population metric comparisons. Because recruitment did not violate parametric assumptions, we did not transform recruitment values. For community metric comparisons, Smith and Wilson Evenness A Index was log-transformed and Simpson's Diversity Index values were not transformed. We present all data untransformed (mean  $\pm$  1 standard error). Because we predicted a direction of effects, we report one-tailed  $P$ -values. We conducted the repeated measure ANOVA in SAS 9.3 [53]. We used R 3.0.1 for Windows [54] for two sample  $t$ -tests, Shapiro–Wilks' tests, Levene's tests (package = lawstat) [77], and NMDS and SIMPER analyses (packages = Ecodist, Vegan, MASS) [78], [79], [80]. We verified NMDS and SIMPER, and conducted ANOSIM,

analyses using Paleontological Statistics Software Package for Education and Data Analysis (PAST) software [55], [56].

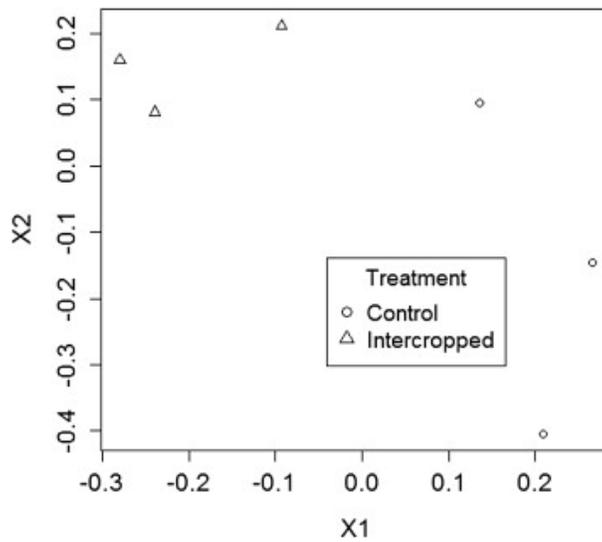
### 3. Results

We had 902 captures of 374 unique individuals from June to August 2012 across 8232 trap nights (intercropped: 4,116, control: 4,116) with equal number of trap nights per trapping period. After trapping commenced, we discovered that one control stand received different site preparation that likely affected vegetation structure, and small mammal traps in one intercropped stand suffered intense raccoon (*Procyon lotor*) disturbance. We removed these replicates from analyses, resulting in 836 captures of 333 unique individuals on 3 intercropped and 3 control stands trapped across 6174 trap nights (intercropped: 3,087, control: 3087) with equal number of trap nights per trapping period. Unique individuals on control stands included 73 hispid cotton rats, 21 *Peromyscus* spp., 3 marsh rice rats (*Oryzomys palustris*), and 2 eastern harvest mice (*Reithrodontomys humulis*). Unique individuals on intercropped stands included 227 hispid cotton rats, 4 *Peromyscus* spp., and 3 marsh rice rats. Hispid cotton rats comprised 90% of all captured individuals while *Peromyscus* spp. comprised 7.5% of all captured individuals. Capture numbers of marsh rice rats, *Peromyscus* spp., and eastern harvest mice were too low for analyses in Program MARK.

We explored possible effects of three stand variables, closest distance to edge (control:  $25.00 \pm 1.53$  m, intercropped:  $48.33 \pm 18.35$  m), closest distance to road (control:  $25.00 \pm 1.53$  m, intercropped:  $55.33 \pm 25.21$  m), and stand area (control:  $35.75 \pm 6.03$  ha, intercropped:  $45.73 \pm 15.78$  ha), on rodent community structure and cotton rat population metrics and observed no significant correlations (data not shown). Therefore, stand variables were not included as covariates in our analyses.

Simpson's Diversity Index ( $W = 0.89$ ,  $P = 0.32$ ) was normally distributed whereas Smith and Wilson Evenness A Index was not ( $W = 0.67$ ,  $P = 0.003$ ). 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 ( $t = 0.39$ ,  $P = 0.57$ ). Smith and Wilson Evenness A Index (intercropped:  $0.05 \pm 0.02$ , control:  $0.41 \pm 0.24$ ;  $t = 2.79$ ,  $df = 4$ ,  $P = 0.02$ ) and Simpson's Diversity Index (intercropped:  $0.05 \pm 0.05$ , control:  $0.40 \pm 0.12$ ;  $t = 2.64$ ,  $df = 4$ ,  $P = 0.03$ ) were significantly lower in intercropped stands than control stands.

Based on the scree plot and a minimum stress of 0.025, we determined a two-dimensional solution for the NMDS was appropriate. The NMDS plot showed clustering of the 3 control stands on one axis and the 3 intercropped stands on the second axis (Fig. 2). Despite clustering on the NMDS plot, the analysis of similarity (ANOSIM) showed no difference between treatments ( $R = 0.81$ ,  $P = 0.10$ ). However, because of a relatively low ANOSIM  $P$ -value, clustering on the NMDS plot, and a relatively low sample size at the plot level ( $n = 3$ ), we proceeded with the SIMPER analysis and found that overall dissimilarity (range 0–100, with 0 = same community structure) between control and intercropped stands was 53.74 with hispid cotton rats contributing to > 86% of observed dissimilarity (Table 3).

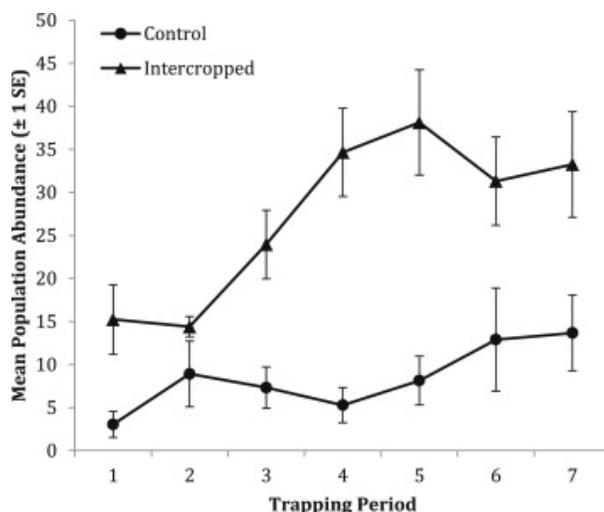


**Fig. 2.** NMDS Plot. Non-metric multidimensional scaling (NMDS) plot of rodent communities by treatment ( $n = 3$ ) in Kemper County, Mississippi, U.S.A. in 2012. NMDS plots show the relative relationships among sites. Stress = 0.025.

**Table 3.** SIMPER results from NMDS. Similarity Percentage results from non-metric multidimensional scaling of pine control stands ( $n = 3$ ) versus intercropped stands ( $n = 3$ ). Contribution is based on the overall dissimilarity of 53.74 and the mean abundances of each species per specified treatment are provided for comparison.

	Contribution %	Mean abundance in control	Mean abundance in intercropped
<i>Sigmodon hispidus</i>	86.13	24.3	75.7
<i>Peromyscus</i> spp.	10.44	7	1.33
<i>Oryzomys palustris</i>	2.286	1	1
<i>Reithrodontomys humulis</i>	1.142	0.667	0

Hispid cotton rat 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 cotton rat survival ( $t = 1.88$ ,  $P = 0.18$ ) and recruitment ( $t = 0.03$ ,  $P = 0.87$ ) whereas cotton rat 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 hispid cotton rats was influenced by treatment ( $F_{1,4} = 16.20$ ,  $P = 0.02$ ), trapping period ( $F_{6,24} = 15.53$ ,  $P < 0.001$ ), and the treatment  $\times$  trapping period interaction ( $F_{6,24} = 5.59$ ,  $P = 0.001$ ) (Fig. 3). Population abundance of hispid cotton rats increased through the trapping season for both intercropped and control stands with abundance increasing more over time in the intercropped stands. There was no treatment effect on hispid cotton rat recruitment (intercropped:  $0.11 \pm 0.03$ , control:  $0.11 \pm 0.02$ ;  $t = -0.07$ ,  $df = 4$ ,  $P = 0.53$ ) or survival (intercropped:  $0.92 \pm 0.02$ , control:  $0.83 \pm 0.08$ ;  $F_{1,4} = 0.41$ ,  $P = 0.56$ ) nor was there an influence of trapping period on survival ( $F_{5,20} = 0.90$ ,  $P = 0.50$ ). Even though the mean response for survival was not significantly different, the standard error was quadrupled in control plots.



**Fig. 3.** Population abundance estimates. Untransformed population abundance estimates (mean abundance  $\pm$  1 standard error) from Program MARK for hispid cotton rats by trapping period. Raw data was obtained from live-trapping (6174 trap nights) using 14,400 m<sup>2</sup> (120 m  $\times$  120 m) trapping grids in control ( $n = 3$ ) and intercropped ( $n = 3$ ) treatments. Seven trapping periods took place from June to August 2012.

#### 4. Discussion

Intercropping switchgrass in intensively managed pine stands altered rodent community diversity and evenness by increasing abundance of the most commonly captured rodent in our study area, the hispid cotton rat. Rodent community diversity was lower in intercropped stands, likely from decreased evenness caused by abundant hispid cotton rats. Our NMDS analysis showed clustering in rodent communities on control and intercropped treatments, and our SIMPER analysis showed hispid cotton rats contributed the most to differences in rodent communities in control and intercropped treatments. Additionally, we did not capture any invasive house mice despite >6000 trap nights across 6 stands.

Our results supported our hypothesis that intercropping switchgrass in intensively managed pine stands would influence rodent population demographics and community structure through differences in forest understory vegetation [25], [57]. Understory vegetation on our research stands differed by treatment [14]. Rodent communities respond to changes in forest structure from different forest management regimes [19], [25], [57], [58], [59], [60], [61], [62]. For example, in intensively managed pine stands 1–5 years post-establishment, total rodent abundance, excluding *Peromyscus* spp., responded to changes in vegetation caused by different intensities of site preparation [60]. Low-intensity site establishment practices resulted in denser vegetation than high intensity establishment, and in greater abundances of eastern woodrats (*Neotoma floridana*), fulvous harvest mice (*Reithrodontomys fulvescens*), and hispid cotton rats [60].

Greater hispid cotton rat abundance in intercropped stands contributed to community dissimilarity between treatments. Intercropping switchgrass in intensively managed pine stands changes the dominant understory structure from woody/herbaceous vegetation to grass [14], thus promoting presence of hispid cotton rats, a herbivore that prefers grass [27], [63], [64]. Similarly,

the hispid cotton rat was the most abundant species in intercropped treatments within the two years after switchgrass establishment in North Carolina, U.S.A [25]. Although, hispid cotton rat survival did not differ between control and intercropped stands, standard error was relatively high in control stands suggesting less variability in survival in intercropped stands.

In addition, presence or absence of coarse woody debris (CWD) can be potentially important for rodent communities [65], [66]. However, the amount of downed CWD after site preparation did not differ between intercropped and control plots on our study area [18]. Even though intercropped plots had fewer retained snags that potentially could become downed CWD [18], CWD does not persist in the southeastern U.S.A. for the length of time that would be relevant to our study [67], [68]. Additionally, removal or retention of coarse woody debris (CWD) in switchgrass/pine intercropped systems has minimal effects on rodent community structure and population demographics in North Carolina, U.S.A [26], [25].

Although rodent community diversity in our study decreased in intercropped stands, the dominant species, hispid cotton rat (75% on control and 97% on intercropped) and *Peromyscus* spp. (20% on control and 2% on intercropped), on both stand types remained the same. Hispid cotton rats dominate rodent communities in young to intermediate age intensively managed pine stands in the southeastern United States [63], [69]. In our study, abundance of hispid cotton rats was significantly higher in intercropped stands, but this species was the dominant rodent across both treatment and control stands. The second most common rodent captured in our study was *Peromyscus* spp., albeit at low numbers. We could not distinguish white-footed mice and cotton mice during our study, but both species are omnivorous and considered microhabitat generalists and thus likely fulfill similar ecological roles [36], [37], [63], [66], [70], [71]. Further, although we did not estimate abundance, survival, and recruitment for *Peromyscus* spp., the lower abundance in intercropped stands suggests a potential effect of intercropping on these species. However, longer term studies would be required to investigate this observation. Regardless, intercropping switchgrass appears to influence the rodent community without altering dominant species.

Our results suggest that planting and maintaining a dense, grass-dominated understory in intercropped stands [14] may extend the period of early succession and thus presence of early successional rodents [63], [69]. After harvest of a mature pine stand, herbaceous vegetation will colonize the newly disturbed site [19] and increases in soft mast and insects from growth of this vegetation typically results in a high abundance of rodents [62]. As the canopy closes about 6–8 years after stand establishment, woody vegetation becomes dominant [72] until canopy closure reduces understory structure and rodent abundance [62], [73]. Our control (early successional pine) stands contained herbaceous vegetation but to a lesser extent than intercropped stands [14]. Therefore, it is not surprising that hispid cotton rats were found to be the dominant rodent species on both stand types during our study. Thus, increasing grass cover through intercropping may benefit herbivorous rodents (e.g., hispid cotton rats) that use early successional vegetation for cover, nesting, and food resources [19].

In our study, house mice were not associated with switchgrass in the absence of agricultural crops in the landscape [25], [74], [75], [76]. House mice were not captured on any of our 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 in the same landscape [21]. In the absence of an abundant food resource, such as agricultural crops, house mice maintain lower population abundances in forested landscapes [21], [69], [75]. Therefore, our results suggest that intercropping switchgrass in intensively managed pine stands does not necessarily promote presence of invasive house mice.

Although we observed effects of intercropping on population abundance of hispid cotton rats, there were not concomitant effects on survival and recruitment. It is likely our limited number of replicates ( $n = 3$  per treatment) precluded detection of small differences in either survival or recruitment that might explain higher abundance of cotton rats in intercropped stands. Alternatively, emigration in control stands could have been higher than in intercropped stands. Although our study included a relatively large sample of trap nights and cotton rat individuals, number of individuals of other rodent species was small. Lastly, our study occurred over three summer months of an approximate 30-year loblolly pine rotation. Thus, there are limitations in both the spatial and temporal scale of our study, and future rodent research should occur over multiple seasons and on more replicates to address these challenges. Despite these challenges, it is important to consider that we examined the rodent community during summer when stand and climatic conditions are most conducive to native rodent species and that the controls in this study are representative of a large number of acres throughout the region. However, effects of switchgrass intercropping in intensively managed pine stands on rodent communities warrants investigation through canopy closure and potentially through an entire even-aged rotation.

## **5. Conclusion**

A switchgrass intercropping system influences rodent community structure via an increase in hispid cotton rat abundance during the early successional stage of loblolly pine stands in the southeastern U.S.A.

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